

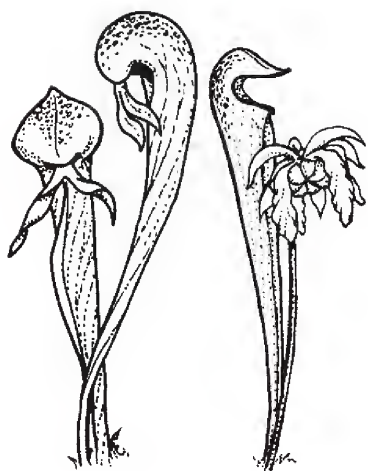
CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

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**Front Cover: Upper pitcher of *Nepenthes* 'Guillermo Reyes'. Photo by Axel Bostrom.
Article on page 215.**

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SEVERAL PYGMY SUNDEW SPECIES POSSESS CATAPULT-FLYPAPER TRAPS WITH REPETITIVE FUNCTION, INDICATING A POSSIBLE EVOLUTIONARY CHANGE INTO AQUATIC SNAP TRAPS SIMILAR TO *ALDROVANDA*

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Keywords: *Drosera*, pygmy Sundew, *Aldrovanda*, *Dionaea*, Droseraceae, Collembola, carnivorous plant, catapult-flypaper trap, snap trap, snap-tentacle, functional morphology, phylogeny.

Abstract: Approximately 50 species of pygmy Sundews (genus *Drosera*, section *Bryastrum*) occur in the South of Australia and one each in New Zealand (*D. pygmaea*) and Venezuela (*D. meristocaulis*). They grow mainly as small stemless rosettes possessing minute trapping leaves of 1-2 mm diameter with prominent marginal tentacles, or have elongated erect stems. The caulescent species possess only mucus-producing tentacles that are most effective in capturing small flying insects. The acaulescent species in contrast are specialized on crawling prey (Verbeek & Boasson 1993) and have developed mucus-free snap-tentacles (Fig. 1), able to bend surprisingly rapidly towards the leaf center. They lift prey like, e.g. springtails (Collembola) from the ground and carry it with a 180°-movement from the periphery of the plant onto the sticky leaf. Our examinations brought to light that several small species of section *Bryastrum* are able to catapult small animals even within fractions of a second. If the whole leaf is touched, several or even all marginal tentacles perform such bending movements simultaneously. We documented this behavior on video, featured on our film “Catapults in Pygmyland” on YouTube (www.youtube.com/watch?v=5k7GYGibdjM). Our results prove that more than only one species in the genus *Drosera* possess rapidly moving catapult-flypaper traps and that the examined pygmy catapults show a further specialization and function repeatedly (in contrast to the one-shot snap tentacles of *D. glanduligera*). The mucus-free and rapid catapult-mechanism functions independent from the initially slow mucilage-based trapping. Furthermore, our study demonstrates that in contrast to *D. glanduligera*, each single pygmy catapult possesses a similar sensor system and hydraulically operated motion-sequences analogous to the lobes of snap-traps. Catapult-flypaper traps submerged in water, forming a kind of grid-cage when triggered simultaneously could be able to capture prey underwater even without any mucilage. This is a possible scenario for the development of aquatic snap traps similar to *Aldrovanda*.

Catapult-flypaper Traps

Very rapid catapulting tentacle movements have only previously been reported



Figure 1: *Drosera callistos* with springtail below the front snap-tentacles.

in the annual *D. glanduligera* (section *Coelophylla*), a close relative of the pygmy Sundews (Hartmeyer & Hartmeyer 2005). These movements, which occur in fractions of a second, are comparable in speed with those of *Dionaea* and *Aldrovanda*. In 2012, we were able to prove in a common project with the Plant Biomechanics Group of the Botanic Garden of the University Freiburg, using a high-speed camera, that *D. glanduligera* utilizes its protruding snap-tentacles to catapult fruit flies (*Drosophila*) within 75 milliseconds (Fig. 2). Activated by the prey's impact, the hit glue-tentacles on the lamina lift the victim within 1-2 minutes into a particularly pronounced patelliform digestion cavity in the leaf center, able to contain 3-4 *Drosophila*. It is a hydraulically driven coordinated two-stage capture mechanism, for which we coined the designation catapult-flypaper trap (Poppinga *et al.* 2012). The catapults of *D. glanduligera* function only once because cells in the hinge-zone burst during the movement through compressive stressing. A slight touch of the tentacle head is sufficient here to trigger a complete bending with maximum speed after a response time of 400 milliseconds. The mucilage producing tentacles show a uniform response time of 8-12 seconds after touching or prey impact. A conspicuous feature of this trap type is that only stimulated tentacles move while the leaf itself remains immobile, it does not curl around the prey. The aim of this study was to determine if tentacles in the pygmy Sundews with a structure similar to *D. glanduligera* react with the same rapidity and exhibit the same behavior as this catapult-flypaper trap and to determine how wide spread this behavior is within this branch of the Droseraceae. For our experiments, we had approximately a dozen plants each of *D. glanduligera* (section *Coelophylla*) and 20 pygmy Sundew species (all section *Bryastrum*) available: *D. androsacea*, *D. callistos* "Brookton", *D. dichrosepala*, *D. helodes*, *D. echinoblata*, *D. eneabba*, *D. enodes*, *D. lasiantha*, *D. leucoblata*, *D. mannii*, *D. microscapa*, *D. miniata*, *D. occidentalis*, *D. platystigma*, *D. pulchella*, *D. pycnoblata*, *D. pygmaea* "Australia", *D. roseana*, *D. scorpioides*, and *D. walyunga*. In addition, Gideon Lim from Malaysia kindly provided us his video of the rapid catapulting action of the all green New Zealand variety of *D. pygmaea*.



Figure 2: *Drosera glanduligera* with just flung fruit fly.

Materials and Methods

We propagated the annual *D. glanduligera* from seeds. Most of the perennial pygmies were only some 8-10 weeks old and grown from gemmae. Some plants are part of our collection since several years (see Table 1). All plants thrived inside our cool greenhouse in Weil am Rhein (Germany) in a southwest location with night temperatures of 4-12°C and 12-26°C during the day. From October to April, we added a 400W HQI-lamp for ten hours daily to complement the low sun intensity during winter. As a reference, some plants thrived inside an adjacent tropical greenhouse with night temperatures of 14-18°C and 22-30°C during the day, applying two 400W HQI-lamps during the same months as mentioned above. Videos and photos: Sony Z5 HDV camera (PAL) with Sony G-Lens. Lumix MH DMC-TZ 10. Microscope: Wiloskop F Zoom (Hund Wetzlar), magnification 13.4-180

Table 1. <i>Drosera</i> species examined and trigger response.	
Examined <i>Drosera</i> species (<i>D. glanduligera</i> = section <i>Coelophylla</i>. All pygmy <i>Drosera</i> = section <i>Bryastrum</i>.) G = grown from gemmae P = perennial plant S = grown from seeds	Catapult motion in relation to <i>Dionaea</i> (0.1 to 2 sec.) (<) slower than (3 to >30 sec.) (~) about equal (0.1 to 1 sec.) (>) faster than (max. 75 ms, recorded in 2012) (--) no snap-tentacles
<i>D. androsacea</i> (G)	<
<i>D. callistos</i> (G)	<
<i>D. dichrosepala</i> (P)	--
<i>D. helodes</i> (G)	<
<i>D. echinoblasta</i> (G)	<
<i>D. eneabba</i> (G)	<
<i>D. enodes</i> (P)	--
<i>D. glanduligera</i> (S)	>
<i>D. lasiantha</i> (G)	--
<i>D. leucoblasta</i> (G)	<
<i>D. mannii</i> (G)	<
<i>D. microscapa</i> (G)	~
<i>D. miniata</i> (G)	<
<i>D. occidentalis</i> (P)	~
<i>D. platystigma</i> (G)	<
<i>D. pulchella</i> (P)	<
<i>D. pycnoblasta</i> (G)	<
<i>D. pygmaea</i> AUS (P)	~
<i>D. pygmaea</i> NZL (?)	~
<i>D. roseana</i> (P)	--
<i>D. scorpioides</i> (P)	--
<i>D. walyunga</i> (G)	<
Remark: Triggered by touching, the initial rapid movement of plants slower than <i>Dionaea</i> stopped often after approximately 45° to 70°, species moving like <i>Dionaea</i> after about 120° to 140°. They needed further touching to complete the bending. With adding fish food, the bending was usually complete (~180°), but the speed differed even for identical species; however, was always the fastest during the first 45°. Due to this behavior and without a high-speed camera, it was impossible to achieve more precise data for maximum movements.	

with iDS CMOS camera UI146xLE-C. Fiber light source FLQ 150 M with gooseneck light guide SHL 250.

In contrast to *D. glanduligera*, fruit flies are too large as prey for experiments with the minute snap-tentacles protruding from leaves with a diameter of only 0.8 to 2 mm. The test plants in our greenhouse spontaneously captured abundant springtails and several mites that occurred naturally in the growing media (Figs. 3 & 4). Photos of *D. glanduligera* *in situ* show quite a broad prey spectrum ranging from springtails and mites to ants and small centipedes of even larger size than fruit flies.

By examining the prey pattern of the co-occurring *D. erythrorhiza*, Watson *et al.* (1982) established that springtails also play a very important role at the natural growing sites. This glue trap with relatively extensive leaves captured mainly Collembola (76%). Moreover, this important nutrient source appears in abundance exactly at the right moment: when the returning rain opens a new growing season and the plants awake from dormancy. Considering 100,000 springtails in one square meter humid soil to be quite usual, Hopkin (1997) gives a measure of their relevance for all *Drosera* with suitable traps.

In addition, Collembola are detritus eaters and like rotting plant debris. Exactly such slowly putrefying leaves are common at the base of many *Drosera* plants. Even the annual and very fast growing *D. glanduligera* develops one new trapping leaf with about 12-18 catapulting tentacles every 3-4 days while the oldest leaves wither correspondingly, becoming a real temptation for detritus eaters. Attracted in such a manner, they touch the snap-tentacles that lie on the ground like the thread sensors of some spiders and are abruptly lifted onto the sticky leaf center.

We conducted an additional experiment inside our tropical greenhouse (now 18-20°C night, 28-32°C afternoon) to examine the behavior of submerged *Drosera* traps. Therefore, an 8-cm pot with green and red *D. capensis* was placed inside a 3-liter plastic tank and slowly submerged with deionized water. We applied two freshly caught houseflies to separate trapping leaves, taking photos after 15, 30, and 60 minutes to document the curling around the prey underwater, and once within 24 hours during the next four days. As the flies do not stick to submerged tentacles, their legs were “hooked” into the tentacles and the bodies were once squashed with a forceps to make them immobile as well as to release some body fluid. Both traps folded around the prey in approximately one hour and remained curled for two to four days, thus indicating that even though submerged, a certain amount of body fluid reached the traps. However, this is only possible without current in standing water.

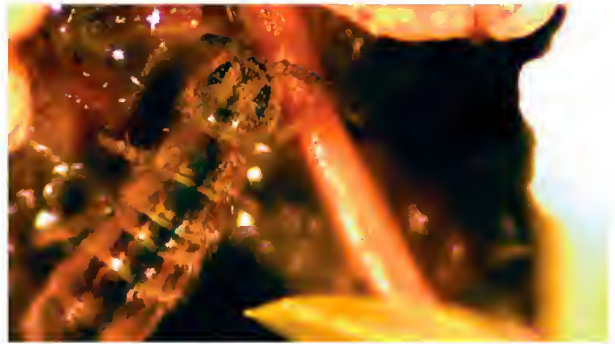


Figure 3: An important food source for small *Drosera*: Springtails.



Figure 4: *Drosera callistos* captured a springtail, which is unable to escape using its furcula (arrow).

Tentacle Movement Experiments

Using a zoom-microscope, we comparatively examined the catapult-flypaper trap *D. glanduligera* and 20 species of pygmy *Drosera* for their tentacle movement. Five species possess only glue-tentacles and grow erect in their course of development. They are obviously specialized to capture small flying insects. Their often far protruding marginal tentacles are also able to bend in the range of several seconds; however, not within fractions of a second (example *D. scorpioides*). Therefore, we limited ourselves to the basal rosettes with glue-free snap-tentacles. To trigger the bending we touched the tentacle heads with a needle.

We carried out the experiments inside a sun-shaded room at a temperature of 22-24°C and artificial 150 Watt LED workplace lighting. Temporarily, when we needed light that is more intense, the temperature underneath the microscope could rise up to 30°C. The test plants came directly from our greenhouse with an afternoon temperature of 20-26°C (see material and methods). As expected, only a slight touch was necessary to trigger a complete and very fast movement with *D. glanduligera*. Its raised tentacle head is unique in the genus (Fig. 5) and works like a foot-switch (Hartmeyer *et al.* 2012). Nevertheless, the compressive stressing destroys the hinge-zone; therefore, each catapult bends only once. In contrast, the snap-tentacles of the pygmy Sundews extend again within a day and function repeatedly. However, it was more difficult to trigger them; especially the 12 larger species often needed multiple hits. Several tentacles did not react, or an initial bending stopped after just a short time. Touching the tentacle head only once was apparently not sufficient for complete bending. With further touching, the movement continues. Presumably, the repeatable functioning catapults, especially in the larger species examined, need quite a few action potentials for a complete 180°-bending. Triggered by a receptor potential that occurs when the sensitive head is irritated, such action potentials are electric impulses, which flow through the plant tissue (Fig. 6). In this particular case, triggered in the tentacle head it actuates a hydraulically powered bending (calculated by Poppinga *et al.* 2012) of the underneath hinge-zone.

To achieve an uninterrupted bending, we decided to add chemical stimuli together with the mechanical. Lichtner *et al.* (1977) refer to Darwin's experiments and mention a response to sodium ion, ammonium ion, and urea. Therefore, we applied minute pieces of crushed fish food flakes (salty protein with traces of ammonium from decomposition) on the tentacle head. The presence of fish food turned out to be a smart move: With very few exceptions, all tentacles reacted after some seconds with a complete bending to the leaf center. Obviously, the chemical stimulation produced a cascade of action potentials causing a complete bending, unlike single mechanical stimulation. However, the speed of the catapults varied even within the same species, but now it was possible to determine the response time between the application of fish food and the start of bending relatively exactly. It is 1-2 seconds for the three smallest and fastest species *D. microscapa*, *D. occidentalis*, *D. pygmaea* and 3-12 seconds for the larger ones.

To apply the minute pieces of fish food, adhering to a needle tip, onto the less than



Figure 5: *Drosera glanduligera* tentacle with raised head (SEM).



Figure 6: Measurement of action potentials on *Dionaea lobata* in 2009 (a rewarded experiment by students of the Friedrich-König-Gymnasium in Würzburg, Germany).

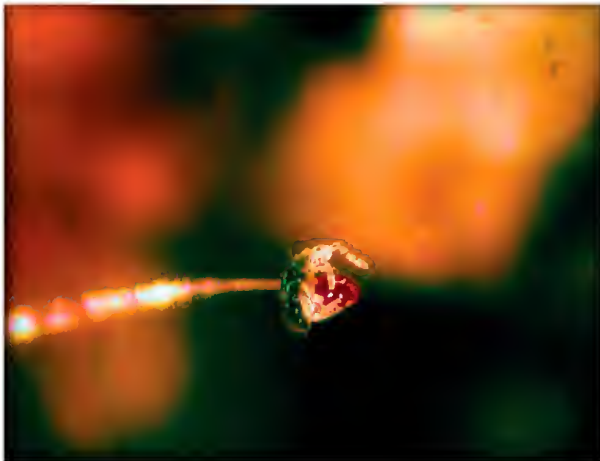


Figure 7: Juvenile springtail sticks to the glue-free snap-tentacle head of *Drosera miniata* in spite of the use of its furcula to escape.

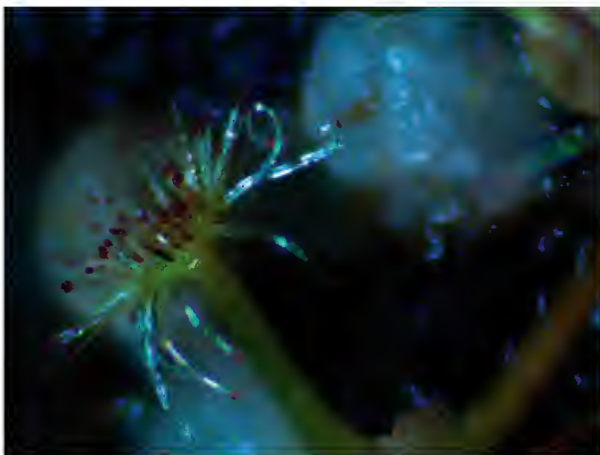


Figure 8: *Drosera enaebba* with snap-tentacles curled by warmth.

100 μm sized tentacle heads under the microscope turned out to be easier than expected. Mostly a slight touch was sufficient and it adhered easily to the mucus-free dry tentacle head. However, in some cases the pieces flipped away rapidly, like being repelled. Such a behavior suggests that electrostatic effects may be involved. If the fish food (crushed inside a plastic lid) had an opposite charge, the tentacle head attracted it and application was easy, while an identical static charge rejected the pieces. During our experiments, we could just coincidentally film a quite small springtail that jumped on a tentacle head of *D. miniata* (Fig. 7). The impact was sufficient to trigger the bending and to lift the prey rapidly from the ground, but then the movement stopped. The action potentials were probably insufficient for a complete bending because the victim appeared to be too small. Surprisingly, even now, the little springtail was not able to release itself from the tentacle. Circling around the head it adhered although it desperately used its catapulting furcula to escape (demonstrated on “Catapults in Pygmyland”). This observation suggests that electrostatic attraction could be involved for prey capture with snap-tentacles. Their speed depends strongly on the condition of the plant and the temperature. Generally, cool nights and moderate day temperatures up to 25°C seem to stimulate a good function. If the temperature is too high, for instance caused by the lighting during the examination, the thin snap-tentacles tend to curl (Fig. 8) and do not bend anymore or only very slowly. Unfortunately, we had no high-speed camera, and the growing and plant conditions in spring 2015 were not optimal. In addition, the 13 species propagated from gemmae (see Table 1) were very young, only about 8-10 weeks old. Bending caused by touching was mostly not complete (180°) and when triggered with fish food we observed varying speed even in the same species. Therefore, it was impossible to de-

termine realistic maximum bending speeds of individual species. However, our experiments allow assessing if a catapult moves faster, in a similar range, or slower than a snap-shutting *Dionaea* trap (about 0.1 to 2 seconds). With catapults achieving the amazing speed of 75 milliseconds (Poppinga *et al.* 2012) for a 180°-movement, so far *D. glanduligera* remains the fastest and largest catapult-flypaper trap in the genus. Its high-performance catapults are clearly faster than *Dionaea*. Speeds similar to the flytrap, with bending in fractions of a second, are achieved by the catapults of *D. microscapa*, *D. occidentalis*, as well as by the Australian and New Zealand variety of *D. pygmaea*. The larger species showed a movement in the range of approximately 3 to more than 30 seconds; these data are, however, most likely unsuitable to establish maximum speed. *D. pulchella* for instance often moved in 10-25 seconds, but once achieved complete movement within approximately 3-4 seconds. *D. enaebba*, *D. mannii*, and *D. miniata* certainly warrant further experiments as they were not in best condition. To determine the fastest movement of pygmy catapults correctly will most likely need observations at their natural habitat. It would be only logical if electrostatic effects between tentacle head and prey affected the frequency of action potentials and thereby the movement pattern. Many species grow on silica sand, diatomaceous earth, or between laterite pebbles. Certainly, such soils charge electrostatically by friction and thereby the soil-dwelling organisms become charged. Silica sand is quartz, well known for its strong piezoelectric effects generated by friction. However, regarding pygmy *Drosera* we found no publications on such phenomena so far.

Results and Discussion

The terrestrial and larger *Dionaea*, which snaps-shut rapidly by a combination of turgor changes that take place in the trap lobes and an elastic instability, is presumably different from the catapulting tentacles of *D. glanduligera* that are small enough to fling prey in fractions of a second solely actuated by hydraulic power (as calculated by Poppinga *et al.* 2012). Remark: Direct measurements on the rate of hydraulic actuation (in case that fast tentacle movement relies additional on a release of elastic energy stored in pre-stressed cells) still have to be undertaken (Poppinga, 2015, pers. comm.).

The features of the catapult-flypaper trap of *D. glanduligera* encouraged us to keep a closer eye at the minute tentacles of the considerably smaller pygmy *Drosera*, focusing at the basal rosettes with mucus-free snap-tentacles. Their rapidly moving structures are only hard to notice with the naked eye; therefore, we examined the cultivated plants with a zoom-microscope.

Our experiments show that in contrast to the erect species in section *Bryastrum*, the acaulescent species do not bend their laminae during prey trapping. Only tentacles are active, exactly as in the closely related catapult-flypaper trap of *D. glanduligera*. Of course, prey-trapping works for all these species often with mucilage only, in this case the catapults remain inactive. Interestingly both mechanisms function independently. Isolated snap-tentacles, which we dissected at the base of the lamina for high-speed filming in 2012, continued to operate properly without the lamina. The action potentials affect only the tentacles and have no connection with the lamina in the species reported by Williams (1976) and very likely these species as well. The tentacles are physically connected just not electrically. Nevertheless, when the catapults are involved, they start a two-stage capture mechanism. The independently acting glue-tentacles perform the second step, no matter if triggered by the impact of the flung prey or a direct touching of an insect. They provide the fixation and correct positioning for digestion like a conveyor belt. This two-stage mechanism is a potential advantage, apparently increasing the availability of nutrients by a larger trapping area in comparison to plants without catapults.

The response time of 8-12 seconds and the 1-2 minutes lasting conveyor belt motion of the sticky apparatus moved at the same level for all examined species. Only the mucus-free catapults



Figure 9: Two catapults of *Drosera occidentalis* moved synchronically.

were able to respond in 400 milliseconds (*D. glanduligera*) up to two seconds, and moved significantly faster. We never found glue-tentacles that bend in fractions of a second. Our observations revealed two distinct and independent acting capture mechanisms in one trap. One is fundamental, mucilage-based and relatively slow; the second appears derived, mucus-free and based on rapid movement. This is of interest regard-

ing the still remaining big question in the Sundew family (Droseraceae): How could initial passive or slow flypaper traps develop into mucus-free fast snap-traps?

The surviving stages of trap development are well known. Simple straight glue traps like the phylogenetically oldest known Sundews *D. regia* and *D. arcturi*, the discussed hydraulic catapults combined with an initial flypaper lamina and eventually the rapid hydraulically powered mucus-free snap traps of *Aldrovanda* and the rapid lobes of *Dionaea* actuated by a combination of hydraulic movement and snap-buckling (Poppinga *et al.* 2013). The thrilling ability of all three Droseraceae genera to capture prey in fractions of a second, started most likely with the development of broad based marginal tentacles in the plane of the leaf. Different from the erect tentacles on the lamina they are additionally equipped with a hinge-zone that contains the necessary motor cells to perform the fast movement. Possibly, they initially still had sticky heads, because all known catapult-flypaper traps still carry a combination of marginal tentacles with and without mucus producing heads. While the erect glue-tentacles on the leaf surface are able to move slowly in all directions, marginal tentacles are restricted to bending up or down due to the broad hinge-zone, but they are very powerful, and rapidly achieve direct hits.

In this respect, it is noteworthy that *D. glanduligera* and the smallest examined species of section *Bryastrum* were able to move two or even almost all catapults nearly synchronically at once (Fig. 9) like a gripping whole hand. When touching a tentacle more intensely, so that the small leaf totters just like touched by larger prey, several catapults are triggered almost at once (documented on our film “Catapults in Pygmyland”). This behavior is certainly effective to capture struggling prey that is too large for one snap-tentacle only. Simultaneously bending catapults can even be able to fix prey without any mucilage because they form first a circular kind of grid cage and act like securing straps after the described gradual narrowing (Fig. 10). If rapid enough, they even capture prey without any glue and push it onto the sessile digestion glands. That is an important advantage in areas with heavy rain, as well as for temporarily submerged plants. Water washes off the mucilage, so the sticky part of the trapping mechanism becomes obsolete. Only the independent rapid capture mechanism remains active to supply animal nutrition. Our study shows that apart from the sessile digestion glands on the lamina, each single repeatedly catapulting tentacle has all properties known



Figure 10: Several snap-tentacles acting like securing straps on *Drosera burmannii*.

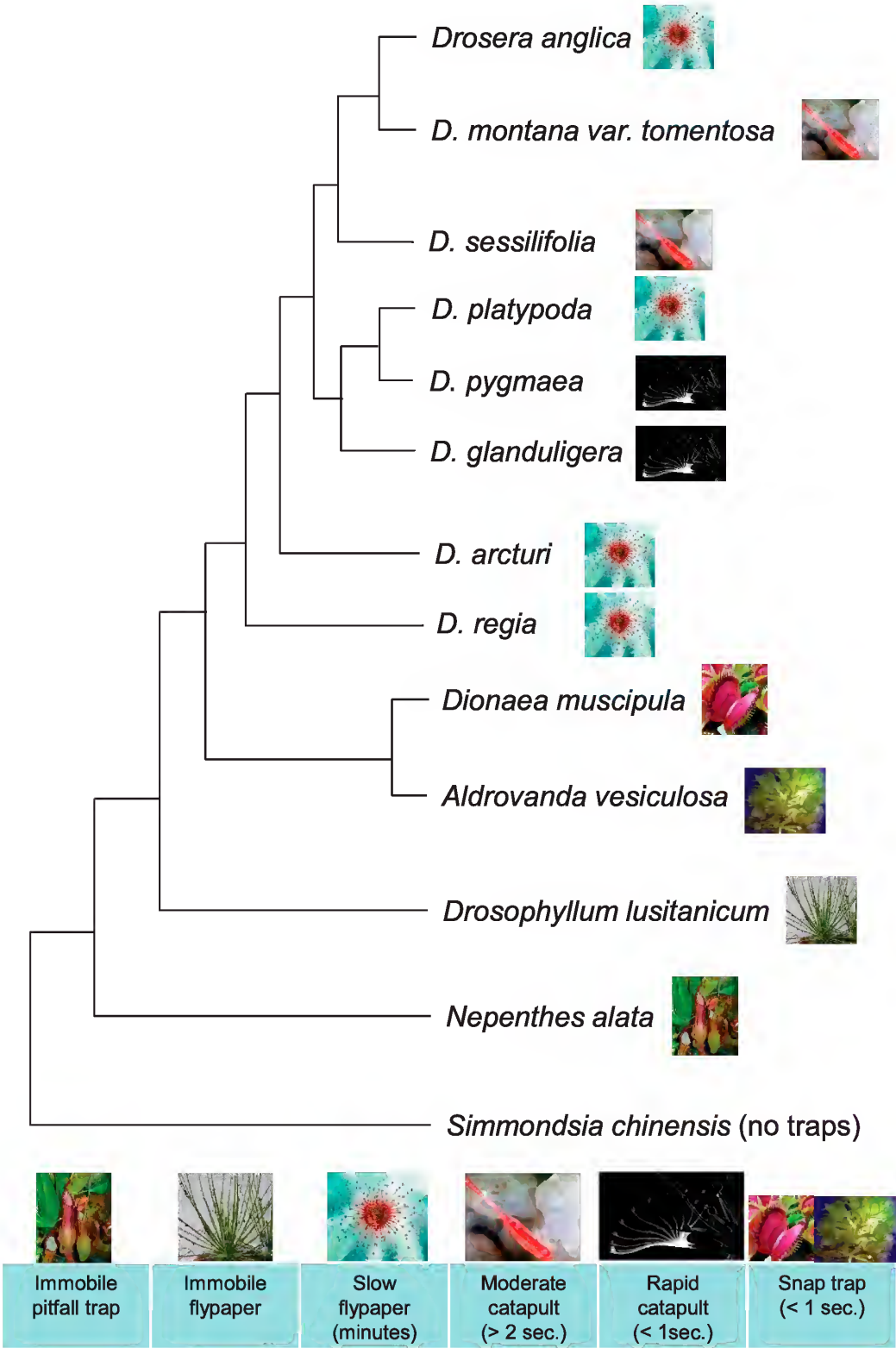
from the trap of the Waterwheel Plant, *Aldrovanda*. Both are touch-sensitive and able to recognize chemical stimuli like ammonium ions or sodium chloride (Williams 1976). Both are able to move initially rapidly as well as gradually for a narrowing by a cascade of action potentials to perform a cost-benefit calculation, deciding to continue/close or to bend back/reopen. *Aldrovanda* lobes show a phase of narrowing after the initial closing: “After the initial rapid closure, the lobes continue moving through a number of phases. After a period of additional slow closure lasting some 30-60 seconds, in which the outer zones of the two lobes press together completely, the free-side lobe becomes concave” (Cross 2012, p. 51). Finally, yet importantly, the existence of *Aldrovanda*, the observations on submerged *Dionaea*, and our own experiments with submerged *D. capensis* (see below) prove clearly that Droseraceae traps function underwater. These facts raise the question: Did an essential change from flypaper traps to snap traps go through an aquatic stage?

Even temporarily submerged *Drosera* able to capture prey with a simultaneously rapid snapping of their catapults have to avoid a loss of nutrition by water flow. Therefore, there is a selective advantage in closing the gaps between the single catapults by merging the bars of the arising grid formed by the tentacles to achieve a sealed digestion cavity to withhold enzymes and nutrition. That would at the same time lead to a perfect simultaneous bending of the now connected catapults, improving the capture of larger prey. Particularly noteworthy in this context is that catapult-flypaper traps like *D. glanduligera* possess a pronounced patelliform digestion cavity in the leaf center, able to contain prey with the volume of 3-4 *Drosophila*, vanishing totally inside. Our experiments conducted in 2012 show that the activated overlying tentacles often notably close the opening after the deposition of prey. Therefore nutrients can be effectively withheld in case of heavy rain or when temporarily submerged. Our experiments in standing water show that even the leaves of *D. capensis* are able to roll in (applied immobile) prey underwater and make use of parts of the nutrients. The leaves remained curled for 2-4 days before they reopened, indicating that a significant quantity of nutrients reached the digestion glands even submerged. Optimizing the closure of the existing large digestion cavity and using the rapid catapults for prey capture would change the former terrestrial or amphibian catapult-flypaper like trap into an underwater working mucus-free snap-trap with lobes. It is that way roughly comparable with a primitive *Aldrovanda* trap. In this perspective, the development of straight snap traps from a *Drosera*-like extinct ancestor of all meanwhile phylogenetically independent Droseraceae clades, possessing simultaneously rapid bending catapults in temporarily submerged areas could be a possible and even plausible event. From an evolutionary point of view, a submerged useless flypaper apparatus became obsolete while the independent acting rapid and mucus-free capture mechanism prevailed successfully (see Table 2).

We do not speculate that initial snap-traps developed from pygmy *Drosera* or looked and functioned like *A. vesiculosa*, which is already highly adapted to straight aquatic conditions. Multifold aquatic snap traps appeared in the past. The surprisingly found trap of the about six million years old fossil of the extinct *A. inopinata* differs in parts. It is for instance lacking the trigger hairs (Schlauer 1997). About 20 other meanwhile extinct species of Waterwheel Plants left only seeds or pollen, so their trap morphology remains unknown. Modern molecular analyses of the chloroplast *rbcL* gene, 18S rDNA, ORF2280 (Williams *et al.* 1994; Fay *et al.* 1997; Lledo *et al.* 1998; Rivadavia *et al.* 2003), and the chloroplast *matK* gene (Meimberg *et al.* 1999) meanwhile provided widely accepted phylogenetic trees, which correspondingly show that the snap-traps appeared in the early phylogeny of the Droseraceae. Surprisingly, these cladograms show a reversal of development, placing the emergence of *Dionaea* and *Aldrovanda* before that of simple flypaper traps like *D. regia* and *D. arcturi*. However, Hosam *et al.* (2009) state that the estimation of genetic distances based on six chloroplast intergenic regions led to the conclusion that the chloroplast genome of *A. vesiculosa*

Table 2.

Cladogram based on the most parsimonious tree resulting from parsimony analysis of the combined *rbcl* and 18S rDNA sequences by Rivadavia *et al.* (2002), supplemented by S. Hartmeyer (2015).



matches more closely to that of *Drosera regia* than its sister genus *Dionaea*. They suspect that the inconsistency between genetic distance estimates based on nuclear and cytoplasmic markers may reflect a chloroplast capture (e.g., by hybridization) because his result is inconsistent with Rivadavia *et al.* (2003) who conclude that the sister relationship of *Aldrovanda* and *Dionaea* indicates a single evolutionary origin of the snap trap system in plants. Nevertheless, Rivadavia states that it was not possible to elucidate which trap system the common ancestor of these lineages had or whether the two systems evolved independently from non-carnivorous plants. Phylogenetic analyses alone provide without doubt acknowledged cladograms; they are, however, not sufficient to establish the correct position of single organisms unambiguously, especially if they are closely related and have only few mutations in the analyzed genes, just like in the case of *Dionaea* and the particular relation of *Aldrovanda* with *Drosera*. A confirmation of the determined position inside the phylogenetic tree by other methods like physiological, morphological, and functional characteristics is necessary. Therefore, the existing cladograms do not definitely clarify whether the aquatic snap trap, the terrestrial snap trap, and the catapult-flypaper traps, all assigned to separate clades, developed independently from one another or not. Considering that, the hypothesis based on our experiments that the aquatic snap trap could have arisen from submerged simultaneously snapping catapult-flypaper-like traps in the early Tertiary or even in the late Cretaceous, can still be considered possible.

Our experiments prove first the existence of several *Drosera* species with rapidly moving catapults, which appear on all cladograms among the phylogenetically oldest Sundews (*D. glanduligera* and *D. pygmaea*) following the simple glue traps *D. regia* and *D. arcturi* (most parsimonious tree, Rivadavia *et al.* 2003). It is evident that each catapult shows the same hydraulically powered movement, identical tactile and chemical sensitivity and even a similar narrowing behavior that occur in *Aldrovanda* and *Dionaea*. Therefore, the current cladogram induced impression of an independent convergent evolution of the three Droseraceae genera from an unknown initial flypaper trap appears in a relative perspective. All Droseraceae genera possess a fast moving apparatus; rapid snapping is not a unique function of snap traps. Nevertheless, the development of rapid catapults from slow mucus-tentacles in *Drosera* is obvious. *Drosera* is the type genus of its family, and it has all structures present in the stalked glands of any of the other members (Williams 1976). A scenario that initial and slow flypaper traps like *D. regia* or *D. arcturi* emerged from *Aldrovanda* or *Dionaea* related snap traps is very unlikely. Considering this, we miss a common ancestor in the early Tertiary or late Cretaceous connecting the initial flypaper Sundews with the rapid catapulting *Drosera*. In this regard, the unique ontogeny of the *D. glanduligera* catapults provides an inside view how evolution acts. Other than the seedlings of more derived *Drosera* species that possess mucus-free snap-tentacles directly after the cotyledons, *D. glanduligera* starts with marginal glue-tentacles. Within about 4-6 weeks, the consecutive new leaves show through intermediate forms an ongoing development until functioning mucus-free catapults result (Hartmeyer & Hartmeyer 2010). That indicates an ancestor with straight flypaper traps in the early Tertiary or late Cretaceous. Unfortunately, it is impossible to complete the existing phylogenetic trees by adding that unknown initial DNA. However, assumed as unknown ancestor for the carnivorous genera in Drosophyllaceae, Dioncophyllaceae, and Nepenthaceae, which divided earlier on the cladograms is a plant that most likely had flypaper traps. It is certainly related with the Droseraceae, as all these genera are members of the order Caryophyllales (Meimberg *et al.* 2000).

Another Possible Area for Future Experiments

Our study shows that the importance of function and interplay of tentacles, in particular *Drosera* traps, is still underestimated and demands further examination. Through our experiments we could

prove that pygmy *Drosera* possess rapid catapult-flypaper traps, but there may be even more species in the genus and highly likely in section *Bryastrum*. To look out for more rapid traps is one field for future experiments, as there are still species with prominent snap-tentacles waiting for a closer inspection from a functional morphological point of view. In addition, the question why fish food and springtails adhere to the mucus-free dry tentacle heads is worth further examination. The receptor and action potentials that trigger the rapid movements result mainly from Ca^{++} -ions stored in the tentacle heads and lobes, thus turning those structures into a kind of electrode. How important are electrostatic effects for prey capture? What role do charged soils like silica sand play? That requires eventually a detailed observation of the traps in their natural environment. Another attempt could be to find the responsible genes for the rapid hydraulic movements for a comparative analysis of all rapidly moving Droseraceae traps. Their phylogeny still raises a number of questions, which demand further experiments.

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SOIL pH VALUES AT SITES OF TERRESTRIAL CARNIVOROUS PLANTS IN SOUTH-WEST EUROPE

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Keywords: Soil water pH, neutral soils, *Pinguicula* spp., *Drosera intermedia*, *Drosophyllum lusitanicum*.

Abstract: Although the majority of terrestrial carnivorous plants grow in acidic soils at a pH of 3.5-5.5, there are many dozens of carnivorous species, mostly mountainous or rocky *Pinguicula* species, which grow preferentially or strictly in neutral or slightly alkaline soils at pHs between 7-8. Knowledge of an optimum soil pH value and an amplitude of this factor may be important not only for understanding the ecology of various species and their conservation, but also for successfully growing them. I report soil pH values at microsites of 15 terrestrial carnivorous plant species or subspecies in SW Europe.

Introduction

The majority of terrestrial carnivorous plants grow in wetlands such as peat bogs, fens, wet meadows, or wet clayish sands. The soils have usually low available mineral nutrient content (N, P, K, Ca, Mg), are hypoxic or anoxic and usually acidic (Juniper *et al.* 1989; Adamec 1997; Rice 2006). Unlike mineral nutritional characteristics of these soils, which have commonly been studied and related to carnivorous plant growth in the field or greenhouse experiments and which have also been published (for the review see Adamec 1997), relatively very little is known about the relationship between soil pH and growth of terrestrial carnivorous plants. Although some limited knowledge of soil pH at habitats of carnivorous plants or in typical substrates exist among botanists and growers (e.g., Roberts & Oosting 1958; Aldenius *et al.* 1983; Studnička 1989; Correia & Freitas 2002; Garrido *et al.* 2003; Adlassnig *et al.* 2006; Rice 2006; Adamec 2009), these items of knowledge are not comprehensive and available for each species and are rather scattered. Even when new carnivorous plant species are described, the pH value of the soil in which they grow is usually not reported (e.g., Casper 2004).

pH value in the soil rooting medium is one of the most important soil factors, comparable with the available contents of macronutrients (Marschner 1995). On the one hand, soil pH tells about the availability of cation exchange of soil particles for H^+ and, on the other hand, it characterizes the ability of uptake of metallic cations from the soil by antiport uptake mechanisms (e.g., K^+/H^+). Moreover, the low soil pH known for the majority of terrestrial carnivorous plant habitats in combination with wet soils (or waterlogging) – i.e., hypoxia or anoxia and low redox potential – can cause both deficiency of some microelements (Mo) and toxicity of others (Fe^{2+} , Al^{3+} ; Aldenius *et al.* 1983; Adamec 1997). In contrast, unusually high soil pH associated with high Ca^{2+} and Mg^{2+} soil contents can lead to soil phosphate precipitation and P deficiency of plants (Marschner 1995). In *Drosera rotundifolia* grown in a diluted mineral nutrient solution differing in pH, Rychnovská-Soudková (1954) showed a principal growth effect of different pH according to the mineral N forms available. Thus, though pH value of wet soils appears to be important for growth of carnivorous plants, only a few manipulative soil pH experiments have been conducted on carnivorous plants so far (Adamec *et al.* 1992; Adamec 1996). Results of these layman greenhouse growth studies, in which a natural peaty substrate was alkalized or acidified by ca. one pH unit using $NaHCO_3$ or HCl, are rather ambiguous but show that certain species may react – positively or negatively – on changes of soil pH.

The majority of terrestrial carnivorous plants grow in acidic soils, but the exact natural soil pH values or the pH amplitudes are known only for several species (e.g., Roberts & Oosting 1958; Aldenius *et al.* 1983; Studnička 1989; Adamec 1996, 2009; Correia & Freitas 2002; Garrido *et al.* 2003; Adlassnig *et al.* 2006). However, within the *Pinguicula* genus, there are several dozens of species growing in neutral or slightly alkaline limestone or dolomitic soils mostly in mountains with their habitats in wet, dripping or sprayed rocks (Rice 2006). They mainly occur in SW and S Europe and Mexico. It is known that some eurytopic, widely spread carnivorous species tolerate rather wide amplitude of soil pH values. E.g., *Drosera rotundifolia* in the Czech Republic was found to grow at pH between 2.9-6.5 (Adamec 1996) and *Pinguicula vulgaris* in N Sweden was reported to grow at pH values of 4.1-6.7 (Aldenius *et al.* 1983); the true pH amplitude can be much wider. On the other hand, an immensely rare Czech endemic lowland species *Pinguicula bohemica*, which is very similar to the former species with which it can co-occur, is stenotopic and only grows within a very narrow range of pH between 6.2-6.9 in base-rich fens (Studnička 1989). It is anticipated that European mountainous *Pinguicula* species occurring on wet limestone or dolomitic rocks (e.g., *P. grandiflora*, *P. vallisneriifolia*, *P. poldinii*) shall grow in alkaline or at least neutral soils. In line, the only pH soil measurement available for *P. crystallina* from SE Turkey shows soil pH of 7.5 (Adamec & Pásek 2000). In this study, I show soil pH values at microsites of 15 terrestrial carnivorous plant species or subspecies in SW Europe.

Methods

Dozens of sites of terrestrial carnivorous plants of the *Pinguicula* genus, *Drosera intermedia*, and *Drosophyllum lusitanicum* were visited during a trip of Czech carnivorous plant growers to SW France, Spain, Portugal, and NW Italy during 26 April – 6 May 2005. As some plant populations did not flower, exact species determination was not possible. Otherwise, the determination was also partly based on pieces of exact information on the distribution of some species (or hybrids) provided by local experts. Exact site names are omitted here for the reason of plant protection. Mixed soil samples were collected using a pair of forceps very close to the root system at each microsite and placed into plastic vials. Usually from 3-5 subsamples from different adjacent plant colonies, ca. 6-12 g of wet mass of a mixed sample was collected at each site. Water pH of the collected soil samples was measured in a laboratory by a pH electrode in soil suspensions (soil:water ca. 1:2 v/v; 5 h). Median and range of values are shown (Table 1). When needed, median was calculated through H^+ concentrations. For comparison, published soil pH data on *Drosophyllum lusitanicum* from Spain and Portugal (Adamec 2009) are also presented.

Results and Discussion

The species studied can be subdivided by their soil pH values into two distinct categories (Table 1). One category, represented by *P. lusitanica*, *Drosera intermedia*, and *Drosophyllum lusitanicum*, can be called as “acidophilous”. These species clearly prefer acidic soils (medians 4.2-5.8), their soil pH amplitudes are rather wide (usually >2 pH units; see also Adamec 1996, 2009), and the upper pH ranges reach medium values of ca. 6.5-7.0. *D. lusitanicum* is a typical example as its total pH range known from the literature is 3.6-7.0 (see Adamec 2009). At several visited sites, *D. lusitanicum* grew at dry, rocky, or stony microsites very close (commonly only 20-30 m) to wet *P. lusitanica* microsites (especially along roads) and, thus, the pH values based on the same substrate were similar. Other typical members of this category are *Drosera rotundifolia* growing at pH between 2.9-6.5 (Adamec 1996) and *P. vulgaris* between at least 4.1-6.7 (Aldenius *et al.* 1983). As these “acidophilous” species usually do not extend to pH of 7.0, they probably cannot grow in slightly alkaline soils. Soil pH values usually correlate with the content of available Ca^{2+} plus Mg^{2+} and, thus, it is accepted that the growth of these “calcifuge” species at medium or

Table 1. pH values of mixed soil samples from microsites in SW and S Europe. ?, uncertain determination of the plants. n, number of microsites. *, data taken from Adamec (2009).			
Species	n	Median	Range
<i>P. grandiflora</i>	2	7.27	7.04-7.78
<i>P. grandiflora</i> subsp. <i>rosea</i>	1	8.04	--
<i>P. grandiflora</i> × <i>P. vulgaris</i> ?	1	5.69	--
<i>P. grandiflora</i> × <i>P. longifolia</i> ?	2	7.23	7.11-7.40
<i>P. dertosensis</i> ?	2	7.20	6.91-8.74
<i>P. mundii</i>	2	7.66	7.54-7.83
<i>P. vallisneriifolia</i>	3	7.74	7.49-7.78
<i>P. longifolia</i> subsp. <i>causensis</i>	2	7.35	7.08-8.27
<i>P. longifolia</i> subsp. <i>longifolia</i>	2	7.17	7.04-7.36
<i>P. longifolia</i> subsp. <i>reichenbachiana</i>	5	7.55	6.90-7.89
<i>P. crystallina</i> subsp. <i>hirtiflora</i>	1	6.90	--
<i>P. poldinii</i>	1	7.51	--
<i>P. lusitanica</i>	7	5.84	4.21-6.57
<i>Drosera intermedia</i>	3	4.21	3.79-5.05
<i>Drosophyllum lusitanicum</i> *	10	4.40	3.67-5.30

higher pH values is rather inhibited by these divalent cations than by pH in itself (Rychnovská-Soudková 1953; Juniper *et al.* 1989).

On the other hand, all the other *Pinguicula* species or their hybrids (but *P. grandiflora* × *P. vulgaris* ?) investigated can be considered “neutrophilous” and/or “alkalophilous” (Table 1). The typical soil pH values are within 7.0-8.0. Theoretically, as a water suspension of milled pure limestone or dolomite should have pH >8.5, the commonly measured lower values prove that the alkaline soil bedrock in the rooting medium was neutralized and acidified by soil organic matter and root exudates. Similarly as in the case of the “acidophilous” species, the pH amplitude was wide 1-2 pH units and could be caused by different proportion of organic matter in the soils which usually occurred on vertical limestone rocks. Moreover, these soils on vertical rocks were mostly only 10-15 mm deep. The results show that “neutrophilous” *Pinguicula* species grow in soils the pH of which never decreases below 6.9. The putative hybrid *P. grandiflora* × *P. vulgaris* indicates that the exceptionally low soil pH (5.7) for “neutrophilous” *Pinguicula* species was influenced by the “acidophilous” parental species *P. vulgaris*.

The results shown in Table 1 should be taken into account when preparing suitable peaty substrates for different plant groups. While “acidophilous” species grow well in acidic, base-poor peaty substrates at pH of 4.0±0.5, the “neutrophilous” species need an addition of ca. 5-10 % (v/v) milled or ground limestone for alkalization of the acidic peat to the pH of >7.0 (Rice 2006).

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IS LONG-TERM SURVIVAL OF DRIED TURIONS OF AQUATIC CARNIVOROUS PLANTS POSSIBLE?

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Keywords: *Aldrovanda vesiculosa*, *Utricularia* spp., winter buds, turion drying and freezing, turion sprouting.

Introduction

Turions of perennial aquatic carnivorous plants of the genera *Aldrovanda* and *Utricularia* are dormant, overwintering buds and are formed by extreme condensation of short, modified leaves in the shoot apex at the end of the growing season (Fig. 1) (Sculthorpe 1967; Bartley & Spence 1987; Adamec 1999). These tough organs represent also storage organs both for carbohydrates and some mineral nutrients (N, P; Winston & Gorham 1979a; Adamec 1999, 2003, 2010, 2011; Płachno *et al.* 2014) and their respiration rate is greatly reduced as compared to that of summer shoots (Adamec 2003, 2008a, 2011). Turions are partly frost-resistant organs which usually overwinter in shallow waters close to the bottom and escape from being included in ice (Adamec 1999). In some species and very shallow habitats, however, turions overwinter also above the water surface in the terrestrial ecophase, on wet organic substrate. Thus, these turions can face both freezing and drying in these microhabitats. Adamec & Kučerová (2013) investigated the characteristics of frost-resistance of turions of 8 aquatic carnivorous plant species and measured the freezing temperature of autumnal, dormant, non-hardened turions (interpreted as freezing of extracellular water) within a range of -7.0 to -10.2°C, whereas the freezing temperature of outdoor hardened turions of 6 species was within a very narrow range of -2.8 to -3.3°C. These characteristics suggest that turions can be hardened by weak frosts and that their hardiness is based on the shift from frost avoidance in non-hardened autumnal turions to frost tolerance in the spring.

Data are available that turions of several *Utricularia* species are able to survive drying and sprout. Maier (1973a) found that *U. vulgaris* turions dried for 1-123 days were able to sprout and grow. However, the older the turions were, the less tolerant of drying they were. Turions refrigerated for five months before being dried out survived very poorly. Turions of *U. vulgaris*, *U. australis*, *U. intermedia*, and *U. minor* were able to withstand drying out (24±3°C, 33% RH) for 5-19 days and, in addition, the drying markedly shortened innate turion dormancy: from 12-48 days in control turions to only 5-7 days in dried ones (Maier 1973b). In another study, Adamec (2008b) found that the survival of spring dried turions was distinctly species-specific: *U. australis* and *U. ochroleuca* s. str. completely survived drying at 3°C for 5 days, but *U. bremii* and *Aldrovanda vesiculosa* did not. *U. australis* showed to be very resistant to drying and survived at 89-100% even a long dry period of 375 days, but *U. ochroleuca* did not at all. Moreover, dried *U. australis* turions even survived (at 100%) freezing at -11°C for 5 days indicating a possibility for a long-term turion survival in dry state. As turions lose major part of their storage carbohydrates over winter (Winston & Gorham 1979a; Adamec 1999, 2003, 2008a), under natural conditions (and also in a refrigerator), they can survive only from one season to another (Adamec 1999, 2003). On the physiological level, the



Aldrovanda vesiculosa



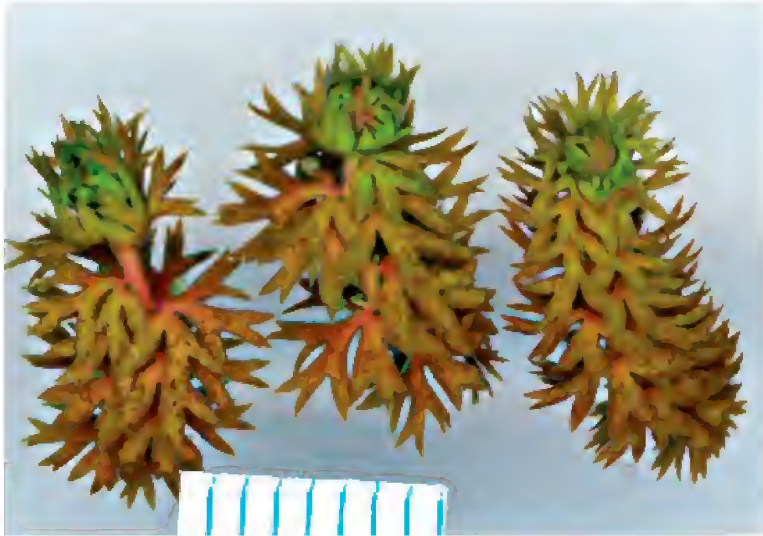
Utricularia stygia



Utricularia vulgaris



Utricularia macrorhiza



Utricularia bremii

Figure 1: Ripe or just sprouting turions of *Aldrovanda vesiculosa*, *Utricularia stygia*, *U. vulgaris*, *U. macrorhiza*, and *U. bremii*.

overwintering and stages of dormancy in *U. vulgaris* turions are regulated by native phytohormones, mainly by the ratio of activities of abscisic and gibberellic acid (Winston & Gorham 1979b).

The aim of this paper was to investigate survival of turions of 6 aquatic carnivorous plant species after long periods of drought in a combination with frost, to test a possibility to prolong the relatively short turion life-span when stored in water in a refrigerator. A protective effect of paraffin oil on turion storage was also tested.

Materials and Methods

Ripe dormant turions of *Utricularia australis* (collected from two different sites from Třeboň basin, S Bohemia, Czech Rep.: humic pool at Ptačí blato and at Pihulík), *U. intermedia* and *U. stygia* (formerly *U. ochroleuca* s. lato; both species from Třeboň basin), and *U. bremii* (from Lake Oniega, NW Russia; the latter three species freshly collected from the outdoor collection of the Institute of Botany at Třeboň) were thoroughly washed by tap water, blotted dry, put on an open Petri dish, and let dry out in a refrigerator at $3\pm 1^\circ\text{C}$ and $59\pm 2\%$ RH for 4 days. On 3 Nov. 2006, dozens of dried turions were put in plastic vials and kept either frozen at $-12\pm 1^\circ\text{C}$, refrigerated at $3\pm 1^\circ\text{C}$ or in darkness at room temperature of 20 to 26°C for 17 months (517 days). After this treatment, 15-20 turions of each variant were put in filtered humic culture water in a miniphytotron at $20\pm 1^\circ\text{C}$ in white fluorescent light (ca. $180\ \mu\text{mol m}^{-2}\text{ s}^{-1}$; 12/12 h L/D) for 26 days to test their survival and sprouting ability. As the turion sprouting of some species was very low indicating that the innate dormancy might not be broken sufficiently by the drying (*sensu* Maier 1973b), turions in the culture water were then put to a refrigerator at $3\pm 1^\circ\text{C}$ for 2 months to break their innate dormancy. After this cold treatment, turions were allowed to sprout in the miniphytotron at $20\pm 1^\circ\text{C}$ in light for another 30 days. Non-sprouting but still living turions were then transferred outdoors and the vials with turions were let floating on the surface of an outdoor growth container in full sun at ca. $20\text{--}30^\circ\text{C}$ for two days. Twenty parallel dried *U. australis* turions (from Pihulík pool) were kept frozen at $-12\pm 1^\circ\text{C}$ for 29 months (882 days), then put in the culture water at $3\pm 1^\circ\text{C}$ for 31 days to break the innate dormancy, and were then allowed to sprout in the miniphytotron at $20\pm 1^\circ\text{C}$ in light. Another 20 parallel dried *U. australis* turions were kept in darkness at 20 to 26°C for 64 months (1936 days) and were then allowed to sprout at $20\pm 1^\circ\text{C}$ in light.

In another experiment on 2 Nov. 2011, 10-20 freshly collected dormant turions of each of *A. vesiculosa* (from SW Hungary, collected from Suchdol nad Lužnicí sand-pit), *U. australis* and *U. bremii* (both latter species taken from the collection) were thoroughly blotted dry, put in a small plastic vial with liquid paraffin oil, and kept refrigerated at $2\pm 1^\circ\text{C}$ for 68-81 days to learn whether this water-free medium can facilitate turion survival at low temperature. They were then blotted dry, put in the culture water and allowed to sprout in the miniphytotron at $20\pm 1^\circ\text{C}$ in light. In another experiment on 11 Dec. 2011, 10 dormant turions of each of *A. vesiculosa* (from E Poland), *U. australis* and *U. ochroleuca* s. str. (from Třeboň basin; all species taken from the collection) were thoroughly blotted dry, put in a small plastic vial with paraffin oil, and kept frozen at $-14\pm 1^\circ\text{C}$ for 72 days. Then, turion sprouting was tested in the culture water at $20\pm 1^\circ\text{C}$ in light.

Turions of all species were scored as sprouting if they distinctly reflexed their basal leaf whorls and partly opened themselves (see Adamec 2003, 2008), and as dead if they were blackened without any sign of sprouting. Although the sprouting of control turions, which were kept standardly in the culture water at $3\pm 1^\circ\text{C}$ in darkness, was not estimated within the above experiments, it is well-known from other experiments and tests (e.g., Adamec 2003, 2008b; Adamec & Kučerová 2013) that the percentage of sprouting at 20°C in light in each species was nearly 100%.

Results and Discussion

Similarly as in the previous study (Adamec 2008b), turions of *U. australis* showed to be the most resistant to long-term drying of all species investigated (Table 1). Dried dormant *U. australis* turions were able to survive both freezing at -12°C and keeping at 3°C for 17 months and fully sprouted afterwards only after additionally breaking the innate dormancy by a next 2-month cold treatment and after exposing to bright light. Thus, as opposed to results of Maier (1973b), who dried and stored turions of 4 *Utricularia* species at a relatively high temperature (24±3°C, 33% RH) for 5-19 days, *U. australis* turions dried at 3±1°C in this study did not break their dormancy at all. However, a weak breaking of dormancy was found in turions of *U. bremii* and *U. stygia* frozen at -12°C. Dried *U. australis* turions could only survive when kept frozen or at 3°C for 17 months, but not at room temperature. In line, parallel dried *U. australis* turions kept at room temperature for 64 months died during rehydration (data not shown). Dried *U. intermedia* turions did not survive the rehydration after both treatments and, except for frozen *U. bremii* turions, the same also applied for turions of *U. bremii* and *U. stygia* (Table 1). Although dried *U. australis* turions were able to fully survive freezing at -12°C for 17 months, they completely died after 29 months of the same treatment during rehydration (data not shown). Thus, a marked species-specificity was found for long-term survival of dried turions at low temperatures.

Table 1. Sprouting of dried *Utricularia* turions originating from outdoor collection but *U. australis*¹, collected from Ptačí blato pool, and *U. australis*², collected from Pihulík pool. First, dormant autumnal turions were dried in a refrigerator at 3°C for 4 days. As a treatment, they were kept dry at -12°C, 3°C, or 20 to 26°C for 17 months. Afterwards, they were put in culture water and allowed to sprout in light at 20°C in a thermostat chamber for 26 d. Then, non-sprouting turions were kept in the water in a refrigerator at 3°C and darkness to break dormancy for next 2 months and allowed to sprout in light at 20°C for 30 d again (sprouting scored after 10 and 30 d). The remaining turions were then transferred outdoors where they could sprout in natural light. (dead), all remaining turions were blackened and dead.

Species	Number of turions	Treatment of dry turions for 17 months	Cumulative number of sprouting turions			
			At 20°C after 26 d	After next 2-month cold treatment at 3°C; in light at 20°C after next		Outdoors full sun (after 2 d)
				10 d	30 d	
<i>U. australis</i> ¹	20	-12°C	0	2	4	20
- “ -	20	3°C	0	8	11	20
<i>U. australis</i> ²	20	20 to 26°C	0 (dead)	--	--	--
<i>U. intermedia</i>	15	-12°C	0 (dead)	--	--	--
- “ -	15	3°C	0 (dead)	--	--	--
<i>U. bremii</i>	20	-12°C	5	0	0	0 (dead)
- “ -	20	3°C	0 (dead)	--	--	--
<i>U. stygia</i>	20	-12°C	3 (dead)	--	--	--
- “ -	20	3°C	1 (dead)	--	--	--

Dormant humid turions of three species (*A. vesiculosa*, *U. bremii*, *U. ochroleuca*) survived being immersed in paraffin oil at 2°C for 68-81 days and sprouted then at 83-100% – comparably with controls (data not shown). Similarly, non-dormant turions of the three species kept under these conditions in paraffin oil for 4 months sprouted at 90-100% (data not shown). However, after dormant humid turions of three species (*A. vesiculosa*, *U. australis*, *U. ochroleuca*) had been kept frozen at -14°C for 72 days, all turions died during rehydration (data not shown). Thus, keeping of blotted-dry turions in paraffin oil in a refrigerator at temperatures above zero or in a frozen state does not render any advantage for turion overwintering and cannot be recommended, though the effect of paraffin oil in itself is harmless.

As found recently (Adamec & Kučerová 2013), dormant, non-hardened wet turions of 8 aquatic carnivorous species froze within a range of -7.0 to -10.2°C and freezing was usually lethal for the turions. Out of all tested species in the present and previous study (Adamec 2008b), the turions of *U. australis* were clearly the most resistant both to drying and freezing of dried turions. Yet, the freezing temperature of both non-hardened (-9.0±0.3°C) and hardened turions (-3.1±0.1°C) of *U. australis* lay near the means for all species and did not indicate at all an exceptionally high frost resistance (Adamec & Kučerová 2013). In line, it is not clear which endogenous factor cause *U. australis* turions to be rather tolerant to long-term drying. Though this species grows also in very shallow habitats and can even survive longer periods of growing in the (semi)terrestrial ecophase on wet substrate (Adamec 2008b), another 4 relative species investigated (*U. bremii*, *U. intermedia*, *U. ochroleuca*, *U. stygia*) normally grow also in the terrestrial ecophase on wet substrate and their turions should be adapted better to occasional drying out and freezing over winter – but they are not.

In conclusion, turions of aquatic carnivorous plants have evolved to survive only a limited, ca. half-year period of unfavorable frosty or cold conditions, i.e., from one season to the next. Therefore, due to their metabolism, their life-span even under ecological, cold overwintering conditions is usually limited to ca. a half year (Adamec 2008a,b). Turions of some resistant species are able to withstand drying at low or room temperature and subsequent keeping in cold even for one year and normally sprout afterwards. Yet, drying of dormant, autumnal turions may not be followed by breaking the innate dormancy (Table 1), while drying of non-dormant, spring turions having been kept at above zero temperatures in a refrigerator may be harmless (Maier 1973b). As shown in this study, a long-term keeping of dormant dried turions either at a low temperature (ca. 2 to 3°C) or frozen at ca. -12°C is not possible (except for common *U. australis*). Thus, a long-term keeping of dried turions of aquatic carnivorous plants at any temperature is not possible and cannot be recommended. A storage using a paraffin oil cannot be recommended, either. The best way to overwinter the turions is to keep them at a very low, above zero temperature (1 to 2°C) under water or in a wet state.

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LITERATURE REVIEW

By John Brittnacher

Bailey, T. 2015. *Drosera* × *eloisiana*, not *D.* × *belezeana*. *Planta Carnivora* 37(1): 42-47.

Camus (1891) described a plant he considered a hybrid between *Drosera rotundifolia* and *D. intermedia* and named it *D.* × *belezeana* after the collector, Marguerite Belèze. Jan Schlauer questioned whether the specimen in the Paris herbarium is in fact a hybrid. He suggested to a number of people that the specimen appears to be *D. rotundifolia* and a new type specimen be selected. Bailey (2015) collected a confirmed *D. rotundifolia* × *intermedia* hybrid in the UK and designated it as the type for the hybrid. He also proposed a new name, *Drosera eloisiana*. However in this situation, current rules of nomenclature (ICN Art. 57.1) demand the preservation of the current name rather than the creation of a new name. Stay tuned; this taxonomic drama is not yet finished. There is more likely to be said in the future.

Camus, E.G. 1891. Note sur les *Drosera*, observés dans les environs de Paris. *Journal de Botanique* 5: 196-199.

HYPOTHESIS OF MUCILAGE-ASSISTED DISPERSAL OF *DROSERA* SEEDS

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Several *Drosera* taxa occur in seasonally wet herbfields on the upper slopes of isolated granite outcrops in inland South Western Australia. These habitats are naturally irrigated by runoff from adjacent rock surfaces. Many of these sundews that grow here, particularly rosetted tuberous sundews (*Drosera* subgenus *Ergaleium* section *Erythrorhiza*) and fan-leaved sundews (*D.* subgenus *Ergaleium* sect. *Stolonifera*) produce spherical seeds around 1 mm diameter that lack obvious surface characters to readily facilitate dispersal to other granite outcrops. Yet these sundews are common components of these habitats in the region. How then did these sundews spread across the landscape when their seed appear to be poor candidates for long-distance dispersal?

It has been suggested that perhaps foraging water birds may have helped spread sundew seeds that have been entrained in mud that temporarily adheres to their feet (Lowrie 1988, pers. comm.). Or seed may be dispersed by strong winds (Lowrie 2014: vol. 1, p. 338). Such events have likely occurred, however another factor contributing to seed dispersal may be at play.

During fieldwork in this part of the world over the last 20 years I have enjoyed visiting granite outcrops where large populations of sundews, such as *D. bulbosa* subsp. *bulbosa*, *D. lowriei*, and *D. macrophylla* subsp. *macrophylla* occur. Curiously many individual populations of *D. bulbosa* subsp. *bulbosa* and *D. lowriei* have remarkably uniform leaf size, shape, and color and which vary noticeably in morphology from adjacent but isolated populations.

On these granite outcrops tuberous sundews often grow sympatrically with a range of other geophytes, including the exotic *Romulea rosea* (Iridaceae). These habitats are frequented by a range of birds, including Galahs (*Eolophus roseicapilla*) that feed on seeds of herbs and bulbs. During my visits I have occasionally observed the dehiscence of some *Drosera bulbosa* and *D. macrophylla* seed directly onto bedewed leaves of the same or adjacent rosettes where the seeds become coated in mucin (Fig. 1).

Mucin produced by the insect-trapping glands on the leaves of sundews consists largely of an aqueous solution of polysaccharides (Rost & Schauer 1977). After desiccation and rehydration the mucin once-again become sticky.

I propose that in addition to the water-bird transport hypothesis, that large round seeds of some sundews have been periodically spread between granite outcrops by other birds, such as parrots. In their search for food they have sometimes had mucin-coated *Drosera* seed adhere to their bodies which they have occasionally transported to other suitable but isolated habitat. Sundew seed may be collected by birds walking directly on live rosettes already with fresh seeds on them. Or perhaps birds walk first on live rosettes, picking up mucin, then onto ground with seeds on it. Or even perhaps birds collect older seeds with a rehydrated coating of mucin?

If correct, this mechanism increases the number of options in which chunky, relatively heavy sundew seeds may occasionally be successfully dispersed to new areas of suitable habitat to found new populations. Such successful dispersal events would likely occur only very rarely but appears to be supported by the presence of greater morphological variation between, rather than within, these isolated populations. This seed dispersal hypothesis may apply to other *Drosera* taxa around the World.



Figure 1: *Drosera bulbosa* subsp. *bulbosa* (and *D. glanduligera*) on a granite outcrop near Hyden. Some seed has been shed directly onto active leaves.

Acknowledgement: I thank Allen Lowrie for discussions on the subject of *Drosera* dispersal that have kept me thinking about this interesting topic.

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PHOTOPERIOD REGULATES CAPE SUNDEW (*DROSERA CAPENSIS*) GLAND SECRETION AND LEAF DEVELOPMENT

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Keywords: carnivorous plant, photoperiod, plant development, *Drosera capensis*.

Abstract: Cape Sundew (*Drosera capensis*), a carnivorous plant that catches flies with sticky mucus, has attracted great interest among botanists and horticulture hobbyists since the Darwin era. But little is known about how this carnivorous plant regulates morphogenesis and organ formation to accommodate environmental changes. In this article we present the relationship between gland secretion of Cape Sundew and photoperiod utilizing various physiological and morphological methods. We show that Cape Sundew grows faster and secretes more mucus under long days than under short days. Under long days leaf length and the blade/petiole ratio increases, leading to increased fly catching capacities. More importantly, in the short term, the rhythm of photoperiod causes Cape Sundew to secrete mucus independent of photo intensity.

Introduction

As one of the most special plant groups, carnivorous plants perform photosynthesis and feed on insects and some large carnivorous plants even prey on birds and small mammals. Darwin believed that a carnivorous plant was one of the most astonishing phenomena in the world (Darwin 1875; Ellison & Gotelli 2009). Carnivorous plants are represented by more than 600 species belonging to 20 genera (Ellison & Gotelli 2001; McPherson 2010). Before the 19th century, the majority of naturalists and gardeners believed that “There were no plants that could eat animals because they had no mouth to eat or stomach to digest” (McPherson 2010). Darwin and his son were strongly opposed by people because nobody believed the existence of carnivorous plants. Despite the opposition, Darwin and his son fully verified by “Darwin-style research” that *Drosera rotundifolia* could catch and digest insects. Carnivorous plants can be divided into three insect-catching mechanisms: 1) catches insects by quick movement (*Dionaea muscipula*), 2) by mucus (*Drosera*), 3) by pit-fall traps (*Nepenthes*). *Drosera* is the most widely distributed genus with the largest number of species and can survive not only in the Asian, European, and American wet lands, but also in the seasonal drought regions in the Southern Hemisphere. Despite numerous species and huge differences in surrounding environment, most *Drosera* live in a non-nutritive acid soil environment where the organic substances are slowly decomposed. *Drosera* catch insects by mucus secretion. When a *Drosera* catches insects with its extremely sticky mucus, its leaf will become bent to wrap the insects and form an external stomach which secretes digestive liquid. In this process, the phytohormone jasmonic acid (JA) plays a major role (Nakamura *et al.* 2013). There are also species which catch insects by both quick movement and mucus. For instance, the tentacle of *Drosera glanduligera*, a sundew from southern Austra-

lia, swiftly catapults prey onto adjacent sticky mucus-tentacles and then digest it (Poppinga *et al.* 2012).

The leaves of carnivorous plants not only perform photosynthesis, but also catch insects. These specialized leaves, however, have low photosynthetic efficiency compared with normal leaves, which is believed to be an adaptation to carnivorous behaviors. A “cost-benefit” model was presented by Pavlovic (2010) to explain this phenomenon. Plants need to predict seasonal changes by perceiving photoperiod signals, and then adjust their growth and development process accordingly (Putterill *et al.* 1995; Kobayashi & Weigel 2007; Harmer 2009). In this paper we show that photoperiod regulates leaf growth and mucus secretion in *Drosera capensis*, providing new insights into our understanding of carnivorous plants.

Method and Materials

Plant culture

Drosera capensis were transplanted into moist soil and covered with moss. For photoperiod experiments, plants were grown in chambers under either long day (LD:16/8 h; light intensity 3500 Lux) or short day (SD:8/16 h; light intensity 3500 Lux). For different light intensity experiments “LD 1/2” was 1800 Lux, and “SD 2 times” was about 7460 Lux. The greenhouse humidity was 50-70% and the temperature was kept at 25°C.

For each treatment, lengths of petiole and blade were measured on more than 3 leaves every week (accurate to 1 mm) and blade/petiole ratio was calculated. In addition, a dissecting microscope (Moticam 2306) was used to observe gland secretion. Both the observation and the measurement lasted more than two months.

Scanning electron microscopy (SEM) method

Fixation: Samples were soaked in FAA fixative (100% alcohol: 50 ml; 37-40%: formaldehyde: 10 ml; acetic acid: 5 ml), vacuumed gently until the samples sank to the bottom, fixed for 12-24 hours, and the solution was changed once. Gradient dehydration: 50% ethanol 20-30 min; 70% ethanol 20-30 min; 90% ethanol 20-30 min; 100% ethanol twice, 20-30 min each. Critical point drying: 6 cycles. Spraying: 15 nm thickness, 90 seconds. Finally, electronic microscope photographs.

Results

Droseraceae leaf morphology

Drosera belongs to the plant family *Droseraceae*. There are great leaf morphological differences among different species. *Drosera spatulata* (Fig. 1B), has spoon-shaped leaves with no obvious boundary between petiole and blade, and its glands are in the distal part. *Drosera pulchella* (Fig. 1C) has a round blade with glands in the distal end, the proximal part is flat without glands. Leaves of *Drosera aliciae* (Fig. 1D) are ligulate-shaped without obvious blade and petiole boundaries, and has glands covering all of the leaf. *Drosera capensis* (Fig. 1A) leaf has an obvious boundary, which was selected as the main experimental material because they were easy to grow and reproduce. The *Drosera capensis* leaf can be divided into two domains (dominant): The proximal part of leaf petiole and the abaxial end blade part (Fig. 1A and E). Glands only grow in the blade and not in the petiole. As shown by SEM (scanning electron microscopy), a gland can be divided into a globular head and a rod-shaped base, which is connected to the surface of the



Figure 1: The leaf morphology of *Drosera*. (A) *Drosera capensis*, white arrow indicates petiole, black arrow indicates blade; (B) *Drosera spatulata*; (C) *Drosera pulchella*; (D) *Drosera aliciae*; (E) *Drosera capensis*; (F-G) *Drosera capensis* inflorescence.

blade (Fig. 3A and D). After full expansion of the leaves, glands begin to secrete mucus (Figs. 1E and 2B) and have the ability to capture insects. After a period of vegetative growth, the plant starts flowering. Their inflorescences are curled and gradually open during the elongation process. This type of bolting could keep flower and pollinators away from the dangerous sticky leaves (Fig. 1F-G).

Long day environment activates gland secretion

Exposed under the LD condition for one week, *Drosera capensis* grew faster than those under SD (Fig. 2A). Leaves were long and flat, which favor catching insects. The gland secreted much mucus covering the head, which was extremely sticky (Fig. 2B). Under SD, leaves were curly and small. There was no or very little mucus on the gland head (Figs. 2C and 3D-F). However, the structure of gland didn't show any significant morphologic difference between LD and SD, except SD gland's diameter is slightly smaller than

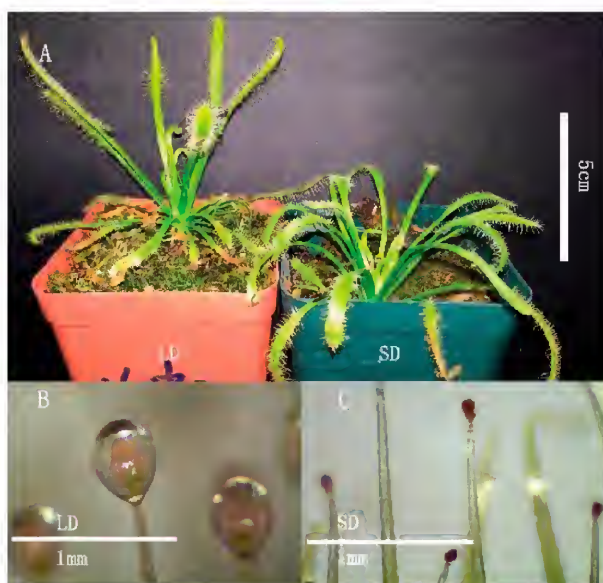


Figure 2: *Drosera capensis* phenotypes (A) under LD and SD. Gland mucus secretion LD (B) and SD (C).

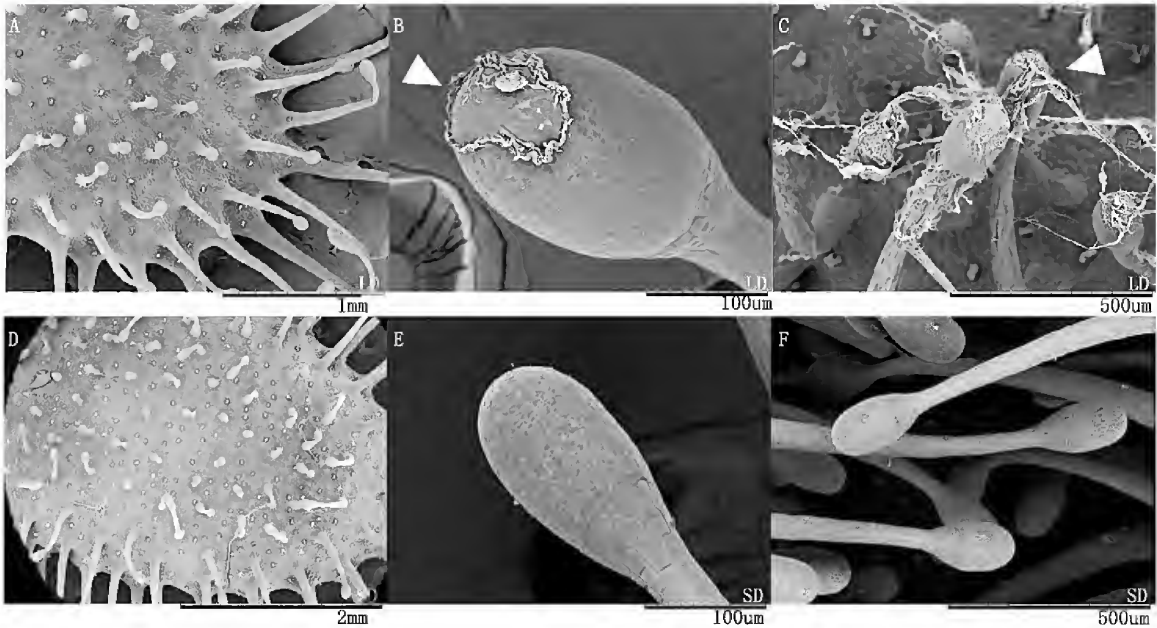


Figure 3: SEM of *Drosera capensis* gland on LD and SD. Leaf on LD (A); the head secreted mucus (white arrow) (B-C). On SD (D), the gland had no significant morphologic difference compared with LD, but there was no mucus on the glands (E-F). The scale is indicated by the black bar.

LD (Fig. 3B and E). The gland on SD still has the secretion function because it secreted mucus again after it was put back to LD for one week.

LD increases the ratio of blade and petiole

The day length not only affects gland secretion in short term, but also could affect leaf morphology in long term. The *Drosera capensis*, which leaf has a ratio of blade and petiole close to 1:1, were put into LD and SD respectively. After two weeks, the blade gradually grew longer than the petiole under LD. However, the plant moved to SD has a longer petiole and shorter blade compared with the LD plant (Fig. 4A), but the full length of the leaf had no statistical difference up to six weeks (Fig. 4B). The newly developed leaves were also measured after 5 weeks. The new leaves on LD have higher blade/petiole ratio and longer full leaf length than SD (Fig. 4C and D).

Rhythm of photoperiod is the main factor affecting gland secretion in the short term in *Drosera capensis*

Different light conditions could cause rhythm difference as well as energy difference. Under LD condition *Drosera capensis* gets more solar energy, which could affect plant development in many ways. To further investigate which aspect of photoperiod plays a more important role, a series of experiments were performed. *Drosera capensis* plants were grown for 6 weeks under LD and SD respectively. Then the SD plants were moved back to LD with full illumination intensity (Fig. 5C and H) and SD with twofold illumination intensity (SD + 2X light) (Fig. 5E and J). The LD plants were also moved to LD with half-illumination intensity (LD + 1/2 light) (Fig 5D and I). After 1 week, plants grown under LD (Fig. 5A and F), LD + 1/2 light (Fig. 5D and I), and from SD to LD (Fig. 5C and H) were able to secrete mucus. The plants grew under SD (Fig. 5B and G) and SD + 2X light (Fig. 5E and J) still haven't had any mucus. All of the results above show that it was the rhythm of photoperiod rather than the quantity of solar energy that regulates gland secretion in the short term.

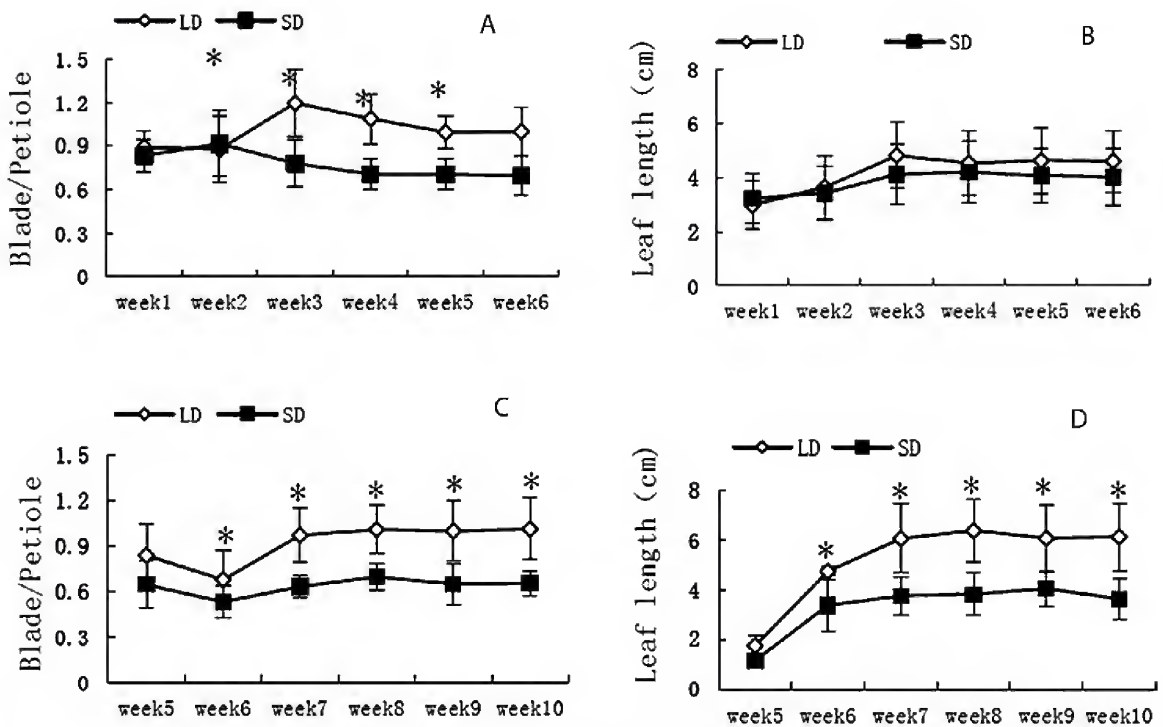


Figure 4: Different photoperiods affect the leaf blade/petiole ratio and leaf length. (A) *Drosera capensis* leaf blade/petiole ratio on LD and SD. (B) Leaf length on LD and SD (number of leaves, N=16-20). (C) The blade/petiole ratio of newly developed leaf on LD and SD. (D) The newly developed leaves length on LD and SD. (* T-test, $P \leq 0.05$. number of leaves, N=18-38).

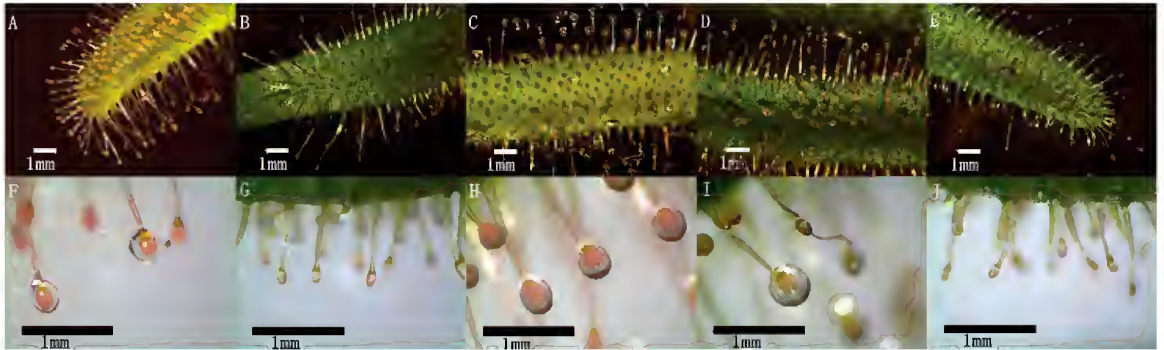


Figure 5: Photoperiod regulates *Drosera capensis* glands secretion independent of illumination intensity. (A & F) on LD; (B & G) on SD; (C & H) on SD moved to LD 1 week; (D & I) on LD moved to LD + 1/2 light 1 week; (E & J) on SD moved to SD + 2x light 1 week.

Discussion

In this paper with different photoperiod and illumination intensity treatments, combined with morphological analysis, we demonstrated that sundew (carnivorous plant) adapts to seasonal changes in different photoperiod environments by regulating the quantity of mucus secretion and adjusting the proportion of insect-catching (leaf blade) and non-insect-catching (leaf petiole) parts. Compared with LD it was obvious that the secretion function of glands under SD was decreased, and leaf blade elongation was also inhibited. After switching from SD environment to LD environment, secretion ability can be fully recovered which indicated that the morphological structure and func-

tion of secretion were normal in both processes of growth. In LD condition, when illumination intensity was decreased by half, the quantity of mucus secretion had no significant change. Similarly, in SD condition, even when illumination intensity was increased by two times, the secreting gland cannot secrete mucus in the short term. The experimental results above indicated that the secretion ability of the secreting gland of sundew was mainly influenced by the rhythm changes of different photoperiods. In addition to the short term effect of mucus secretion, growing in SD environment for a long time, the sundew had obvious phenotypes such as short and curled leaf. Moreover, the proportion of leaf blade was less than for the LD plant.

It's crucial for carnivorous plants whether insects can be caught. Mostly, carnivorous plants grow in the environment where there is a lack of nutrition and cannot meet the demand of absorbing elements such as N and P by the root. Therefore, the carnivorous plants catch insects instead of root nutrient absorption to maintain growth. The same as normal plants, carnivorous plants also forecast and feel seasonal changes through rhythm changes of photoperiod. The glandular secretion of leaf mucus is the only weapon for sundews to catch insects. In an environment where seasonal changes are significant, the quantity of insects is usually rare in winter. At this time, it's not worth consuming too much energy to grow insect-catching organs and secreting a lot of mucus. However, in spring and summer there are plenty of insects in the environment and sundews can secrete a lot of mucus at this time to catch a lot of insects to meet the demand of fast growth. In addition to sundews which can regulate mucus secretion initiatively, pitcher plants were also reported to have passive regulation. When dew drops gather on the peristome of pitcher plants (*Nepenthes rafflesiana*) it will become unusually smooth, which makes it easier for ants to fall and increases the opportunity to catch insects. However, the existence of dew drops depends on external moisture variation (Bauer *et al.* 2015). As for Venus flytrap (*Dionaea muscipula*), it also has the ability to adapt to seasonal changes. The Venus flytrap leaf grows along the ground and the petiole of expands in winter, while the trapping lobe which is in charge of catching insects is smaller and loses the ability to close, which makes it hard to catch insects (unpublished observation).

Compared with normal plants, carnivorous plants need to prioritize between photosynthesis and getting nitrogen resources. Photoperiod regulates the mucus secretion and leaf morphogenesis of sundews, which provides a new research direction to study this issue. Since Darwin's day, carnivorous plants have been studied extensively. The results obtained by modern biology will help people to further understand carnivorous plants.

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SECOND BRIEF PIECE OF INFORMATION ABOUT THE SPECIES STATUS OF *UTRICULARIA CORNIGERA* STUDNIČKA

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Keywords: *Utricularia cornigera*, bladderwort, hybrids, bladders, traps.

Abstract: Hybrids of *Utricularia nelumbifolia* × *U. reniformis* (and vice versa) were raised, and the bladders of adult individuals taken out of the soil were observed. With their long antennae they resemble their parents, yet they differ noticeably from the identically situated bladders of *U. cornigera* that has characteristic short antennae. Therefore, the morphology of the bladders does not support the hypothesis of a hybrid origin of *U. cornigera*.

Introduction

The seedlings from the artificial cross-breeding of *Utricularia reniformis* × *U. nelumbifolia* (and vice versa) documented in CPN 2 years ago (Studnička 2013) have become adult plants, and thus it was possible to document the traps of the hybrids. In this study, a comparison is made with both the parental species and with *U. cornigera*, for it is a species related to both cross-bred species. The species *U. cornigera* and *U. reniformis* are similar to each other with their kidney-shaped leaves. The species *U. cornigera* and *U. nelumbifolia* have symbiotic relationships to host rosette-forming plants (Studnička 2011). All the three species are endemic to south-eastern Brazil.

Material and Methods

The hybrids described in the previous brief information (Studnička 2013) were investigated. These plants have been raised and continue to be kept in the Liberec Botanic Garden. Stolons with bladders were removed from the soil and placed into a small bowl with water. The live material was observed and photographed with a microscope at 16-times magnification. The mounts were made in such a way that the antennae were as visible as possible. In the case of *U. nelumbifolia*, traps from an aquatic environment were observed as this species does not grow in soil. Traps from a soil environment were documented and compared in the case of all the other species and hybrids. In each case, 10 mounts were observed and as no significant variability was ascertained, one representative photograph at a time is included in this article.

Results and Discussion

Protrusions growing out of the throat towards the front of the trap mouth, referred to as antennae (Taylor 1989), are usually considered (*inter alia*) to be a characteristic feature of each species of the genus *Utricularia*. Their shape is apparently associated with the strategy of hunting microscopically small prey and with some specialization (Lloyd 1942). Soil traps specialize in soil microfauna of various composition, whereas water traps are adapted to hunting zooplankton. With respect to the

species *U. reniformis*, the difference between soil and water traps (if they are created at all) is more in the size of the bladder than in the shape and proportionate length of the antennae. By contrast, *U. cornigera* is characterised by marked dimorphism of the traps: water traps (Studnička 2009) have relatively long antennae; soil traps, by contrast, also displayed herein (Fig. 1), have very short ones, reduced to small “horns” (*cornigera* = horned).

In the species *U. reniformis* and *U. nelumbifolia* no traps with short antennae are known at all, and the antennae always go beyond the stalk of the bladder (Fig. 2). It is also the same case with their F1 hybrids created by reciprocal cross-breeding (Fig. 3).

Conclusion

The soil traps of the hybrids created by the artificial cross-breeding of *U. nelumbifolia* and *U. reniformis* do not resemble the soil traps of the relative *U. cornigera* at all. There is no predisposition towards short antennae either in the hybrids or in the parental species. This implies that this

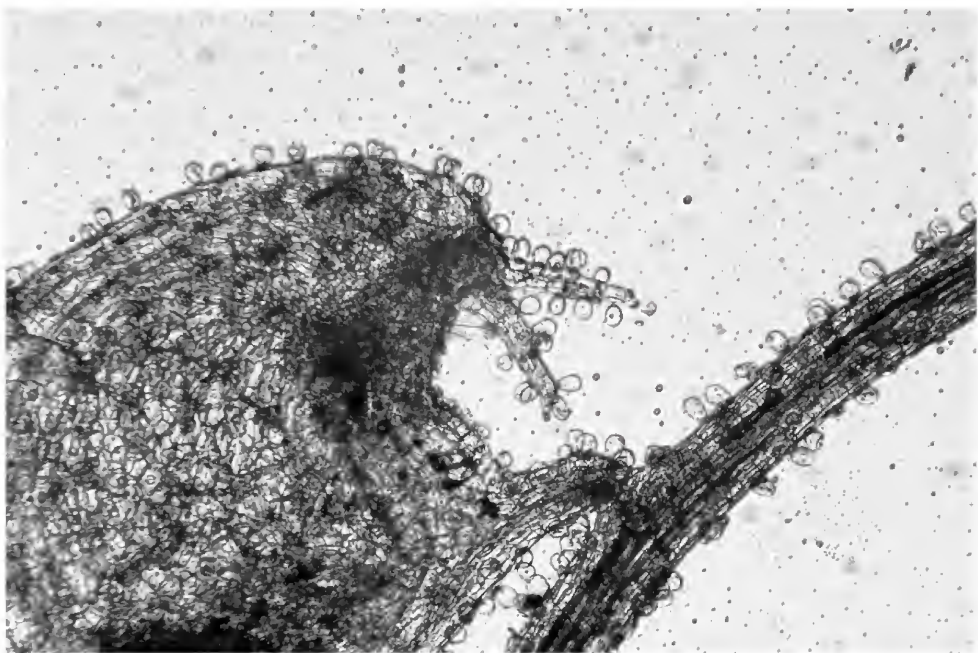


Figure 1: Very short antennae on the soil vesicle of *Utricularia cornigera*.

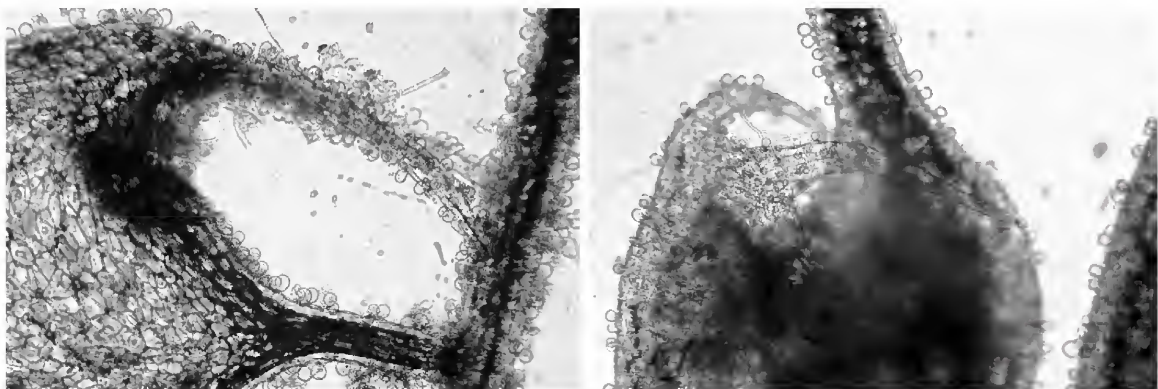


Figure 2: Very long antennae on the bladder of *Utricularia nelumbifolia* (left); and a soil vesicle of *Utricularia reniformis*, where the antennae extend to the stem (right).

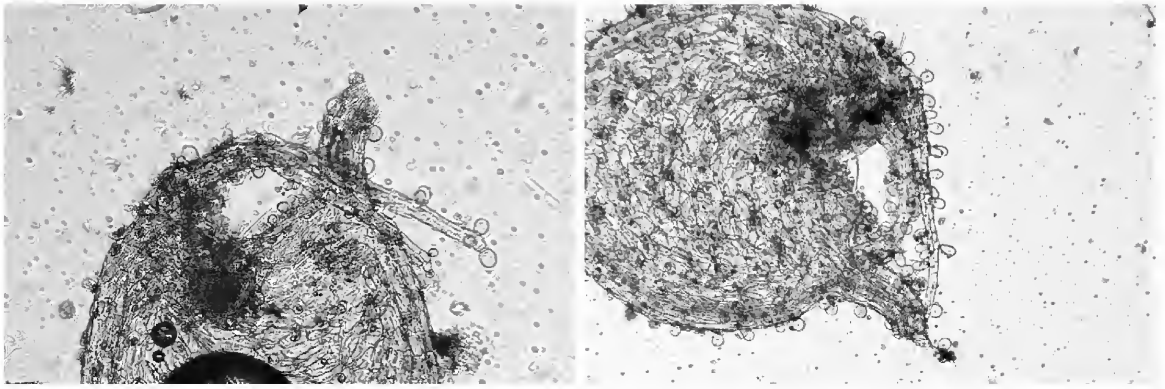


Figure 3: Very long antennae on the soil vesicle of *Utricularia nelumbifolia* ♀ × *U. reniformis* (left); and very long antennae on the soil vesicle of *Utricularia reniformis* ♀ × *U. nelumbifolia* (right).

characteristic feature present in the species *U. cornigera* has apparently developed by evolution. It is not possible for the difference between the hybrids and *U. cornigera* to have been caused by environmental effects because all the plants had identical conditions. The above investigation again refutes the hypothesis of a possible hybrid origin of *U. cornigera*, which was a stimulus for creating the hybrids documented herein.

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HOW HUNGRY ARE CARNIVOROUS PLANTS? AN INVESTIGATION INTO THE NUTRITION OF CARNIVOROUS PLANT TAXA FROM THE KIMBERLEY REGION OF WESTERN AUSTRALIA

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The Project

The pristine Kimberley region in the north of Western Australia is a global centre of carnivorous plant diversity, well known for its abundance of *Drosera* (ca. 20-30 species), *Byblis* (four species), and *Utricularia* (at least 30 species). New taxa continue to be discovered here on a regular basis. As carnivorous plants tend to prefer sunny, moist and nutrient poor environments, the tropical monsoon climate and poor soil fertility of the Kimberley region have allowed for significant diversification of these carnivorous plant genera. The Kimberley sits on a geologically ancient landscape, with naturally old and well-weathered parent rock material and highly leached soils, thanks in part to very high levels of rainfall during the summer monsoon. From May to October, the Kimberley region experiences a hot and often fire-prone dry season, which is followed by a short but unpredictable wet season from November to April. During the 4-5 month wet season it is not uncommon for the region to experience frequent lightning storms, intense tropical cyclones and large flooding events, with rainfall in northern coastal regions during this short period frequently exceeding 2000 mm (around 80 inches). Subsequently, access during the wet season can be extremely difficult, with many areas simply remaining inaccessible until the cessation of seasonal rains.

The nutrition of carnivorous plants is an endlessly fascinating topic, especially given that these plants are able to absorb supplementary nutrients by attracting, capturing, and digesting insect prey with their specially modified leaves. Many aspects of the nutrition of carnivorous plants have been studied in great detail, with Schulze *et al.* (1991) pioneering the use of stable isotope techniques to determine how reliant West Australian species were on capturing insect prey to meet their nutritional needs, as opposed to gaining nutrients through root uptake. While this research shed some light on twelve *Drosera* species from the southwest region of Western Australia, there has been no similar research conducted on the carnivorous taxa of the Kimberley region. This is where my (LS) PhD project comes in, based at the University of Western Australia and Kings Park and Botanic Garden, Perth, Western Australia.

In order to gain an understanding of the nutrition of a wider variety of the carnivorous plant taxa that occur naturally throughout Western Australia, we proposed to expand upon the work of Schulze *et al.* (1991), with a broader range of species surveyed and greater replication. We began this project with a field trip to a remote area of the Kimberley, to collect samples under scientific license of carnivorous plants, non-carnivorous reference plants, potential insect prey, and soil. These samples will be used to determine nutritional differences between carnivorous plant species, and compare this to underlying site characteristics. Our team's research, and particularly the costs associated with remote field study, is funded by grants from Murdoch University, Kings Park and Botanic Garden, the Friends of Kings Park, and the International Carnivorous Plant Society. What follows is an account of our journey to this wonderful part of Australia and how we went about making our collections.

The Journey

To be perfectly honest, in the weeks leading up to this field trip, I was a little apprehensive. The last time I'd been on a serious field trip was nearly two years prior, but add to that the fears that many people associate with the Australian outback: ending up lost in the vast remoteness of the Kimberley (some 423,517 km² of predominantly uninhabited wilderness), suffering dehydration or heat shock, being poisoned by snakes, waking up covered in spiders, or eaten by a giant crocodile. In the wise words of Russell Coight "out here, survival is the name of the game. Only it's not a game; it's deadly serious". With a lot of preparation and a fair amount of luck, we survived our own "All Aussie Adventure" and now it's time to tell the tale!

Our journey began in late March, towards the end of the Kimberley's wet season, in the town of Kununurra. Here, sadly, the invasive cane toad species *Rhinella marina* L. (Bufonidae) has made its mark. For those that may not be aware, the cane toad was introduced to northern Queensland in 1935 in an ill-fated attempt to eradicate problematic cane beetles, and has been steadily working its way across the monsoon tropics ever since. Unfortunately, this plan has resulted in much of our native fauna falling victim to the poisonous cane toads. This was my first time seeing these creatures in person, and, I've got to say, they aren't pretty! Some other wildlife we were much happier about getting acquainted with included the TaTa lizard (*Lophognathus temporalis*), so called for the wave goodbye it does with its front legs after racing away from threats, and the beautiful big boob trees (*Adansonia gregorii*). This is definitely a place that I would like to see a bit more of one day, and maybe even climb to the top of the local hill, Bob's Knob! However, after one night's stay, we were off the next morning to our remote north Kimberley field site; a large pastoral station surrounded by pristine bushland, where we would be spending the next week.

Given that our field site is so very remote and the roads are inaccessible during the wet season, the only feasible form of transport was to charter a flight on an aptly named 12-seater Cessna Caravan (Fig. 1). We placed our luggage amongst the packages ready to be delivered to the many remote stations along the way, and strapped ourselves in. Seeing the Kimberley from a bird's eye perspective was a definite highlight, with my favourite view being that of the Pentecost and Durack River delta, with its winding pathways and incredible colours (Fig. 2). However, it was certainly nice to find ourselves landing at our final destination, returning to solid ground and breathing some of the freshest air I've ever encountered.

Upon landing at the station, we were greeted by its caretakers, Wendy and Bruce, and their dog Bonnie, a beautiful Ridgeback-Dingo cross. First of all, I cannot thank the caretakers enough for their hospitality and generosity, and I'm also very grateful for Bonnie the dog, who became our best friend and fieldwork companion for the week (Fig. 3). We were given a quick tour of the station: the caretakers' and owner's homes had beautiful gardens with fruit trees; the nearby shed was fully equipped to make sure everything ran smoothly, including the quad bikes we would be using to



Figure 1: Our charter Cessna Caravan.

travel between sites each day; and the dongas (small portable rooms) where we would be sleeping were located right next to showers and cooking facilities. For a moment, it was easy to forget that we were staying out in the middle of nowhere... that is, until we found the frogs hanging out in the toilet and geckos crawling in the cupboards! Wildlife was not uncommon, with the howls of a dingo (*Canis lupus dingo*) in the distance, bats flying about the garden at night, a poisonous taipan (*Oxyuramus scutellatus scutellatus*) in the shower, and a big black whip-snake (*Demansia papuensis*) that was spotted near our dongas! These surprises within the pastoral station made the experience all the more exciting, and left us wondering what surprises would await us out in the pristine bushland. We got ourselves settled in for a good night's sleep, ready for the proper fieldwork to start bright and early the next morning.

The Fieldwork

Given we would be conducting our fieldwork in a remote and somewhat dangerous environment, safety was obviously our number one priority. Firstly, to avoid getting lost and to keep track of where we were in the landscape, our fieldwork leader Dr. Adam Cross carried a GPS and EPIRB at all times. Secondly, to keep safe from the hot and sunny environment, we always took plenty of water. Thirdly, we were covered from head to toe with wide-brimmed hats, long-sleeved clothing, hiking boots, sunglasses, and lots of sunscreen. Finally, to protect ourselves from snakes hiding in the tall grasses, we wore knee-high gaiters. Of course, our fieldwork companion Bonnie the dog roamed about the landscape without any worries, as if it were her personal kingdom; drinking from the rivers, resting in the shade, and chasing away any form of wildlife that we encountered, including a young dingo, a big Monitor lizard (*Varanus panoptes*), and a stubborn group of feral cattle (*Bos taurus*).

In order to get to our sites, we each drove a quad bike loaded up with all of our equipment and water, and made our way through the tall grasses, over rocks and dead tree branches. Riding about on those quad bikes was a whole lot of fun, and it's something I really miss now that I'm back in Perth and not out in the field! We would always stay on one track so as to reduce disturbance to the natural landscape, with Adam leading the way. Unfortunately for Adam, this meant he was pelted with spiky Sorghum grass seeds far more than the rest of us, and at one point managed to drive



Figure 2: The Pentecost and Durack River delta.



Figure 3: Bonnie the dog and Laura Skates.

through a large spider's web and ended up with both the web and the spider wrapped around his face! Bonnie often ran at the head of our quad bike conga line, but always doubled back to check on the last person and make sure the whole pack was okay. Over the course of the week Bonnie ran nearly 100 km, so it's no wonder that at the end of each day she would stubbornly request a lift back on the back of the last quad bike through the station's gate. Driving back to the station slowly, with Bonnie curled up behind me, was the best way to end a tough day out in the field!

Over the course of the week, we collected samples of more than ten different *Drosera* species and two *Byblis* species, across nine different sites. We also encountered several *Utricularia* species, although these were not collected as they were outside the scope of my PhD research. Unfortunately, there will have been several species that we missed, as many are quite transient in nature and only present on the landscape for a few weeks each year. Some are expected to flower for only a few days, especially given the relatively dry wet season this year. For the species that we could find, samples of leaf material were collected at each site, along with samples of non-carnivorous plant species to be used as a nutritional reference. Samples of insects and soil were also collected at each site, as these are the two major sources of nutrients for the carnivorous plant species. All of this was very exciting for me, not only to be successful in making my first collections for my research, but also to see such an incredible array of carnivorous plant species, each with different and simply beautiful life-forms.

Many of the carnivorous plants sampled occurred on shallow sands in some variation of an open herb field, surrounded by tall *Sorghum* grasses and a few *Eucalyptus* trees, adjacent to the aprons of sandstone outcrops. Open fields of *Byblis filifolia* were very common and occurred at seven out of nine sites, always accompanied by a handful of other carnivorous plant species such as *B. rorida*, *Drosera banksii*, *D. burmannii*, *D. cucullata*, *D. dilatato-petiolaris*, *D. fragrans*, *D. glabriscapa*, *D. paradoxa*, and *D. subtilis*, as well as several yet-to-be-formally-described *Drosera* taxa. Several of these species were easy to locate, with their bright purple and pink flowers, such as *Byblis filifolia* and *Drosera fragrans*. However, for many of the smaller *Drosera* taxa, such as *D. banksii* and *D. burmannii*, it was necessary to get down on hands and knees in the mud and push back the low herbs and grasses to find the dewy plants hiding beneath. As you might expect, we would often find a greater abundance and diversity of carnivorous plants at the edges of pristine sandstone creeks (Fig. 4) running through the herb lands, where soils were moister. In these areas, *D. banksii*, *D. cucullata*, and *D. paradoxa* in particular were more common.

While driving our quad bikes from one site to another, we stumbled upon a particularly interesting patch of herb land, where we spotted a different *Drosera* species. Spread like a carpet along the dry soil of this sandy herb land was *Drosera ordensis*, a gorgeous perennial species in which the white, hairy petioles contrast strongly with the blood red trapping leaves (Fig. 5). This was the only carnivorous plant species found growing in this area; perhaps the sand was too dry for the predominantly annual species that we had previously found on more moist soils. Another reason as to why this site was of particular interest was the presence of a nearby



Figure 4: Sandstone creek running through herb lands.

cave painted with Aboriginal rock art. Indigenous Australians have occupied the Kimberley region for nearly 40,000 years, and continue to be the traditional owners of the land. Many Aboriginal groups still practice traditional law in this region, as part of one of the world's oldest continuous cultures. We were incredibly lucky to have the opportunity to see this ancient artwork, and it is something that I will not soon forget.

One of the most exciting days on the field trip by far required us to cross a large river to get to our field site (Fig. 6). That's right, we stripped down to our bathers, lowered ourselves into the murky waters of the Kimberley, and crossed our fingers that there would be no crocodiles! Our fieldwork leader assured us that it would be perfectly safe; usually, crocodiles don't come this far inland. Even if they did, this particular area of the river was too shallow and rocky for their liking and located between two waterfalls, which crocodiles tend to avoid at all costs. Of course this just made me think of the possibility that a crocodile could have somehow made its way this far inland, got itself stuck between these two waterfalls, become enraged by the rocks scraping against its belly, and would be just about ready for a tasty meal. Crikey!

It was very reassuring that Bonnie jumped in the river without a care in the world, and swam back and forth the whole way while waiting for us to get our equipment ready. This was the real challenge: transporting all of our sampling gear, hiking boots, lunch, and expensive cameras across the river, without them all becoming soaked or lost at the bottom of the murky waters! We placed everything into rubbish bags



Figure 5: *Drosera ordensis*.



Figure 6: Our crossing at the Morgan River.

and big plastic crates, which we floated out in front us as we swam the distance, Bonnie by our side. Luckily, we made it across the river without any harm and without any loss of equipment. I'm not going to lie, I felt a bit like Crocodile Dundee!

Once we'd made it to the other side of the river, the adventure was not over. We still had to trek our way across the sandstone and woodland and collect our samples. After a somewhat rainy lunch with a beautiful view, we found ourselves trapped under a fast approaching lightning storm. In such a remote place, lightning can be a big problem, as fires can be started quite easily. With our equipment, including my metal pole with an insect net attached to the end, we were basically a beacon for any stray lightning that might occur. We hurried off to find shelter under a large boulder overhang, to keep us (and Bonnie!) safe and dry.

Once the storm had passed, we were able to resume our work, and collected a variety of species including *Byblis filifolia*, *Drosera glabriscapa*, *D. serpens*, and *D. subtilis*. The rain continued to drizzle over us all day, making it quite difficult to take notes on wet paper, and leaving us soaked to the bone. As the daylight started to fade, we began heading back towards the river crossing area and prepared ourselves for the swim back to the other side. Floating our crates of equipment across was even more difficult this time around, thanks to the extra weight of all of our samples, but we made it in the end! While this day on the fieldtrip was definitely the most exciting, we were all glad to be returning to the station to dry off.

On our very last day of sampling we ventured into some swampy blacksoil areas by the roadside in the hopes of finding a few species that had been quite elusive throughout the earlier days of the trip. Success! We found *Drosera hartmeyerorum*, *D. nana* and *Byblis liniflora* growing in the shade of other herbaceous plants, small shrubs, and *Eucalyptus* trees, as well as the more prevalent species *D. banksii*, *D. burmannii*, and *D. fragrans*. Many of these species grew right up to the edge of the roadside, where vegetation began to thin out, perhaps exploiting the higher light available. Having collected as many different species as we possibly could, we returned to the station and began the arduous task of packing away all of our equipment and samples in preparation for the long journey home – a job that lasted well into the early hours of the next morning.

Final Thoughts

Once the trip had come to an end, I was able to reflect on the success of the field work, the difficulties involved in the sampling process, and the exciting adventurous aspects that we had the privilege to experience. Over the course of one week, we were able to get a significant amount of sampling done for my PhD project: nine different sites, collections of nearly 20 different carnivorous plant species, a total of 250 plant samples (including the non-carnivorous plant samples for reference), 30 collections of potential insect prey, and about 5 kg of soil. Through this process, I was also able to determine the best methods for collecting, sorting, and labelling my samples, which will come in very handy when I go to collect other carnivorous plant species in the southwest corner of Western Australia – an even more exceptionally biodiverse region harbouring more carnivorous plants than anywhere else on the planet. The next step will be to analyse and compare all of the plant, insect, and soil samples, to determine whether there are differences in the nutrition of species from different families and from different geographic locations. Until then, I feel extremely lucky to have been able to see such a great range of the native fauna and flora that makes the Kimberley region of Western Australia so unique, and I hope I can return to this beautiful part of our country again one day soon!

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NEW CULTIVARS

Keywords: cultivar, *Drosera intermedia* 'Éclat', *Dionaea* 'Coquiton', *Nepenthes* 'Guillermo Reyes'

Drosera intermedia 'Éclat'

Submitted: 31 August 2015

Drosera intermedia 'Éclat' was found in August 2012 among a full container of *D. intermedia* of wild type plants (Fig. 1 left) obtained from Cédric Azais from which the cultivar developed (by mutation). Unlike the typical form, *Drosera intermedia* 'Éclat' has a lack of red coloration (Fig. 1). Otherwise, the plant is similar to *D. intermedia*.

The name "Éclat" comes from the brightness of the mucilage.

I have successfully propagated the plant by seed and leaf cuttings.

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Figure 1: *Drosera intermedia* 'Éclat' surrounded by typical reddish *Drosera intermedia* (left) and a clump of *Drosera intermedia* 'Éclat' (right).

Dionaea 'Coquiton'

Submitted: 24 August 2015

Dionaea 'Coquiton' is totally green but can verge on yellow. It is prostrate and compact, with arched traps, reminding one of *Dionaea* 'Cudo'. The petiole is short and large and sometimes there is an excrescence on it. The teeth are short, stocky, the tip of the teeth is curved and/or deformed, bringing the tentacles of *Drosera* to mind, and there are intermediate microteeth (Figs. 2 & 3).

The name *Dionaea* 'Coquiton', coined 23 September 2014, is a combination of the names of the parents: *Dionaea* 'Coquillage' × *Dionaea* 'Triton'. The plant should be reproduced only by vegetative means to ensure that its unique characteristics are maintained.

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Figure 2: *Dionaea* 'Coquiton' plant.



Figure 3: Arched trap and the short deformed teeth of *Dionaea* 'Coquiton'.

Submitted: 21 August 2015

Nepenthes 'Guillermo Reyes' is a seed grown *Nepenthes platychila* obtained from Borneo Exotics. I have grown this plant for the past 5 years and have not seen another *N. platychilla* quite like it. I named this special plant *Nepenthes* 'Guillermo Reyes' on 10 July 2015.

Leaves of this plant are covered in short, bronze-colored hairs. The new leaf emerging from the terminal node will often appear completely bronze in color. There is a distinctive bronze line beginning at each auxiliary node, extending through the mid-rib of the leaf (Fig. 4).

Lower pitchers are green, heavily blotched with red and purple, and have a red striped golden peristome (Fig. 4). Upper pitchers are absolutely fantastic, large, and robust with a similar blotched pitcher body as the lower pitchers, however, the peristome flares out quite far, and is covered in hundreds of ruby red colored stripes (Front Cover).

This cultivar is named after Guillermo Reyes, a long-time friend and excellent *Nepenthes* grower who has dedicated his life to this hobby.

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Figure 4: The new leaf emerging from the growth point appears completely bronze (left); bronze hairs make a very obvious line down the mid rib on each leaf (center); and lower pitcher of *Nepenthes* 'Guillermo Reyes' (right).

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